

INSECTES SOCIAUX

UNIVERSITY OF HAWAII
LIBRARY

MAR 9 '57

BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX



COMITÉ DE RÉDACTION

J. D. CARTHY, P. H. CHRISTENSEN, K. GÖSSWALD, P.-P. GRASSÉ,
C. JUCCI, A. RAIGNIER, T. C. SCHNEIRLA, T. UCHIDA

Volume III - Octobre 1956 - Numéro 4

MASSON & Cie ÉDITEURS - PARIS

PUBLICATION PÉRIODIQUE TRIMESTRIELLE.

INSECTES SOCIAUX

Revue consacrée à l'étude de la Morphologie, de la Systématique et de la Biologie des Insectes sociaux.

Publiée sous les auspices de

L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX

COMITÉ DE RÉDACTION

J. D. CARTHY, Department of Zoology, Queen Mary College, Mile end Road, London E1 (England).

P. H. CHRISTENSEN, Universitetets Institut for almindelig Zoologi, Universitetsparken 3, Copenhagen, Denmark.

K. GÖSSWALD, Institut für Angewandte Zoologie der Universität, Würzburg, Röntgenring 10, Würzburg, Deutschland.

P.-P. GRASSÉ, Laboratoire d'Évolution des Êtres organisés, 105, boulevard Raspail, Paris-VI^e, France.

C. JUCCI, Istituto di Zoologia « L. Spallanzani », Pavia, Italia.

A. RAIGNIER, 11, rue des Récollets, Louvain, Belgique.

T. C. SCHNEIRLA, American Museum National History New-York (U. S. A.).

T. UCHIDA, Zoological Institut Faculty of Sciences, Hokkaido University Sapporo, Japan.

PRIX DE L'ABONNEMENT POUR 1956

France et Union Française : **3 000 frs.**

Étranger { Dollars U. S. A. : **9,25.**
 { Francs Belges : **460.**

Également payable au cours officiel
dans les autres monnaies.

Prix spécial pour les membres de l'Union Internationale pour l'étude des Insectes sociaux.

France et Union Française : **2 000 frs.**

Étranger { Dollars : **5,75.**
 { Francs Belges : **286.**

Règlement : a) Chèque sur Paris d'une banque officielle.
 b) Virement par banque sur compte étranger.
 c) Mandat International.

ADMINISTRATION

MASSON et C^{ie}, Éditeurs

120, boulevard Saint-Germain, PARIS-VI^e

° °

SECRÉTAIRE

M. G. RICHARD

105, Boulevard Raspail, PARIS-VI^e

INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE
POUR L'ÉTUDE DES INSECTES SOCIAUX

SOMMAIRE

Mémoires Originaux.

The natural density of <i>Myrmica Rubra</i> and associated ants in West Scotland, by M. V. BRIAN	473
Notes on the ant genus <i>Holcponera</i> Mayr, with descriptions of two new species, by William L. BROWN, Jr.	489
Les facteurs qui gouvernent la ponte chez la reine des Abeilles, par Rémy CHAUVIN	499
Observations on the gastral digestive tract in the male Carpenter ant, <i>Campopnotus Pennsylvanicus</i> degeer (Formicidæ, Hymenoptera), by James FORBES.	505
Beobachtungen über die Gynandromorphen Honigbienen, mit besonderer Berücksichtigung ihrer Handlungen innerhalb des Volkes, von Shoichi F. SAKAGAMI und Hiroya TAKAHASHI	513
Some factors affecting the survival of odontotermes Badius, by W. A. SANDS, M.Sc.	531
The foraging behavior of honeybees on hairy vetch, foraging methods and learning to forage, by Nevin WEAVER	537

Nouvelles de l'Union.

Travaux des membres de l'Union	551
Congrès d'Entomologie de Montréal	558
International Union for the Study of Social Insects North American Section.	561
Table alphabétique des auteurs	563
Table des matières contenues dans le Tome III 1956	566

INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE
POUR L'ÉTUDE DES INSECTES SOCIAUX

Comité de Rédaction :

J. D. CARTHY, P. H. CHRISTENSEN, K. GÖSSWALD, P.-P. GRASSÉ,
C. JUCCI, A. RAIGNIER, T. C. SCHNEIRLA, T. UCHIDA

TOME III

N° 4

MASSON & C^{ie}, ÉDITEURS
120, boulevard Saint-Germain, PARIS-VI^e

1956

I

MÉMOIRES ORIGINAUX

THE NATURAL DENSITY OF *MYRMICA RUBRA* AND ASSOCIATED ANTS IN WEST SCOTLAND

By

M. V. BRIAN

*(Zoology Department, University of Glasgow and the Nature Conservancy, Furzebrook
Research Station.)*

INTRODUCTION

The measurement of the population density of ants is no easier than that of other animals even though their colonies are usually relatively sedentary. Indeed, the difficulties encountered resemble those that the plant ecologist faces, the principal being perhaps to decide what is a unit, for the colony which is the immediate level of organisation beneath the deme is by no means always easy to recognise. That it is a poikilothermic organism, the largest produced by invertebrate animals, is not disputed for it has all the properties of such: coherence, internal regulation, organisation, trophic independence, and the power to reproduce itself in several ways; but the organisimal units are often far from distinct. In certain species division, and in others fusion occurs, and all stages of this indeterminacy may be present at one time, a fact which has led some investigators to use the individual as a population unit rather than the colony. Ideally of course both approaches should be combined and the numbers and weights of workers, queens and all the brood stages and their distribution should be ascertained for only in this way is some knowledge of the quality of the population obtained without which the quantity is a dangerously simple abstraction.

In this study which is partly a re-assessment of earlier work, partly new, population has been measured in terms of colonies for most of the species considered have unusually distinct and frequently monogynous colonies. The size of these has been measured as the number of workers, or more roughly, as small (nanic workers and queens seen on examination), medium (large workers abundant, queens usually not seen, sometimes male sexual brood) and large (as medium except that sexual female brood is always present). In extensive rather than intensive work, the size has not been measured at all and sometimes in these cases even tests of colony difference (by mixing in the laboratory) have not been made, for experience has shown that these ants rarely construct more than one solarium (the above-surface erection by means of which a nest is located). All the work was done in the same area: on the south facing slopes of the sandstone hills between the River Clyde and Loch Lomond.

INSOLATION AND ANT QUALITY

The dependence of many but by no means all ants on direct solar radiation for warmth is well established. Thus there is the comprehensive work of STEINER (1947) and of RAIGNIER (1948), the latter of which has shown the important role that insolation plays in the thermal economy of *Formica rufa*. Even tropical species may need it, or at any rate use it in their thermal economy—as with species of *Anoplolepis* (WAY 1953).

The effect of insolation on the populations of *M. rubra* has been fully treated elsewhere (BRIAN and BRIAN 1951). Little more need be said except to point out that the method of multiple regression used in the second section of the discussion in that paper is unsuitable as the index of insolation (symbolised Y) is clearly an independent variable whilst the other two, mean worker head width (X) and colony size (Z) are dependent. The method used on page 308 (*ibid.*) indicated that much of the variation in worker size was due to variation in insolation quota. When this is applied to colony size the standard equation of regression,

$$Z = 0.38 y + 0.27$$

is obtained but neither coefficient is significant, although the influence of insolation is greater.

Pursuing the problem in another way *, one may set up three reasonable models:

$$Y \begin{matrix} \nearrow X \\ \searrow Z \end{matrix}, Y \rightarrow X \rightarrow Z, \text{ and } Y \rightarrow Z \rightarrow X,$$

in which the arrow symbolises the word “influences”, and test whether the correlation coefficient between the terminal variables bears any relation to the product of the intermediates. Thus, since

$$ryx = 0.852, \quad ryz = 0.611, \quad rxz = 0.594,$$

one finds that with the first model that $ryx \cdot ryz = 0.521$ which is near to ryz ; with the second model $ryx \cdot rxz = 0.506$ which is less than ryz ; and in the third case $ryz \cdot rxz = 0.363$ which is far removed from the value of rxz . The last may with reason be rejected but the two others should be retained for further consideration.

A third test involves calculating the regression of X on Y and of Z on Y and then finding the deviations of each item from these; if they are correlated, X and Z may reasonably be supposed to be directly related, but otherwise only indirectly through Y. The coefficient obtained, + 0.17 is small and non-significant and hence the first model appears most suitable. This thus agrees well with the other result obtained (*ibid.*

* For this and the next method I am indebted to Professor G. W. Snedecor and his colleagues.

p. 306) except that the apparent independence of worker size and colony size is surprising. Examination of Fig. 1 of the earlier paper gives the explanation however: it is seen that the two regress most strongly in small colonies (less than 250 workers) and very little in larger ones. Since the smallest colony considered exceeded 100 workers and they ranged to over 1,000 it is not surprising that the interaction between worker and colony size was not apparent. The conclusions of the final paragraph of the discussion (*ibid.*) are thus fully supported; one may merely add that as colonies grow, the importance of the interaction between worker and colony size decreases, and the effect of insolation increases.

THE CLOSURE OF A GLADE

In the earlier paper circumstantial evidence pointed to the fact that as the trees of a pine plantation grew up and the canopy closed the colonies regressed, became smaller with smaller workers, showed slower brood maturation, and produced fewer or no sexual adults (that is, they were of low fertility as colonies). Further, the workers, instead of collecting juices from aphids living in or near the nest, were found to ascend the trees for it so that the colonies became literally etiolated and far more than the usual amounts of energy must have been spent on food collection. Moreover, the capture of prey which is likely to be a process with an optimum temperature, may easily have been more difficult. In all these ways, some reminiscent of plants under similar circumstances, the quality or vigour of the population was inferior under the low insolation quota.

The population of a closing glade in a mixed spruce-pine plantation has now been investigated in some detail (Fig. 1). The trees to the N.E. were spruce (*Picea abies* (L.) Karst) whilst those to the S.W. were pine (*Pinus sylvestris* L.) and when first examined the vertical projection of their canopy gave a glade area of 38.2 m². The ground was level except for a ditch 30 cm deep with banks of excavated soil (running S.W.—N.E. through the centre) and a few other irregularities never more than 1 m above the general level. The principle floor vegetation was *Succisa pratensis* Roench, *Gallium hercynicum* Weigel, *Potentilla recta* (L.) Räusch, *Anthoxanthum odoratum* L., *Agrostis tenuis* Sibth., *Thuidium tamariscinum* (Hedw.) B & S—near ditch, *Rhytidiadelphus squarrosus* (Hedw.) Warnst—on the drier bank tops. Under the tree canopy this flora gave way to:—*Rumex acetosella* L., *Athyrium filix-femina* (L.) Roth., *Dryopteris spinulosa* (Mull) Watt. In the W. corner *Pteridium aquilinum* (L.) Kuhn was associated with the pines and spread slightly and diffusely into the open glade. The glade held 45 nests of four species of ant: *Formica fusca* L. (1 nest), *Leptothorax acervorum* Fab. (2 nests), *Myrmica scabrinodis* Nyl. (24 nests) and *M. rubra* L. (18 nests) (1). The gross density was

(1) The names used in previous papers are adhered to for clarity. In fact from the recent work of Yarrow (1954, 1955) it appears that *F. fusca* L. is really *F. lemani* Bondroit, and *M. rubra* L. is really *M. ruginodis* Nyl.

1.18 nests per m^2 . The *fusca* nest was under the only stone, the *acervorum* nests were in old tree stumps and the *Myrmicae* nests were widely distributed throughout the remaining area although sparser in the S region where the pine shadows fell. *M. scabrinodis* was more frequent on the bank top than *rubra*, a segregation which though typical was only partial.

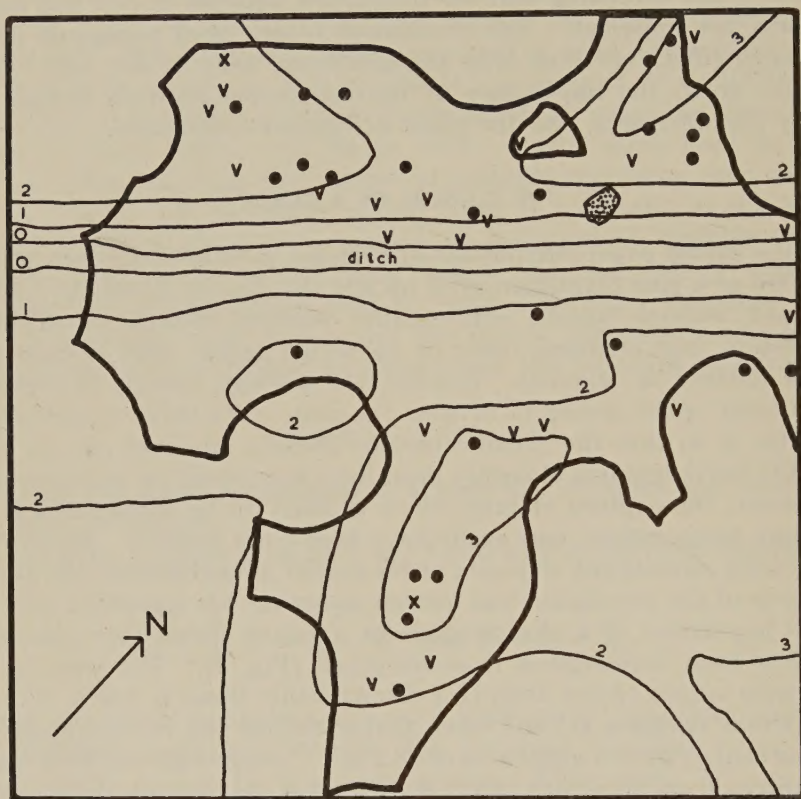


FIG. 1. — The pine-spruce glade at first; contours in feet from zero at the top of the ditch; canopy vertical projection indicated as a thick line; black circles, *M. scabrinodis*; v, *M. rubra*; x, *L. acervorum*; and dotted is the stone with *F. fusca* nest.

Only three nests lay outside the canopy projection: 2 *rubra* and 1 *scabrinodis* and none of these were more than 30 cm outside.

Four years later the area of the glade (Fig. 2) had been reduced to 20.7 m^2 that is 54 % of its initial area and in June the sunlight fell on the floor for only two hours, roughly 13.00-15.00 GMT. The ground herbs were dominated by luxuriant *Succisa pratensis* which was apparently shading out the *Potentilla erecta* and *Gallium hercynicum* and possibly also the moss *Thuidium* and the grasses. Except for one small and notable area of grass about 1 m^2 in area in the centre, grazed by rabbits and carrying uniquely *Lysimachia nemorum* L., none remained. The bottom of the ditch held a rich growth of *Mentha* sp. with, at the sides, straggling

Lonicera periclymenum L. In the W. corner the bracken had luxuriated, reaching heights of 1.5 m and covering 6.1 m² of the non-canopy zone as well as the canopied areas but not crossing the ditch at all. Under the spruce at the N. E. end the *Succisa pratensis* persisted sparsely, the ferns were more frequent and larger, and *Oxalis acetosella* L. had appeared.

Only 9 ant nests could be located: 1 *fusca*, 5 *scabrinodis* and 3 *rubra*,

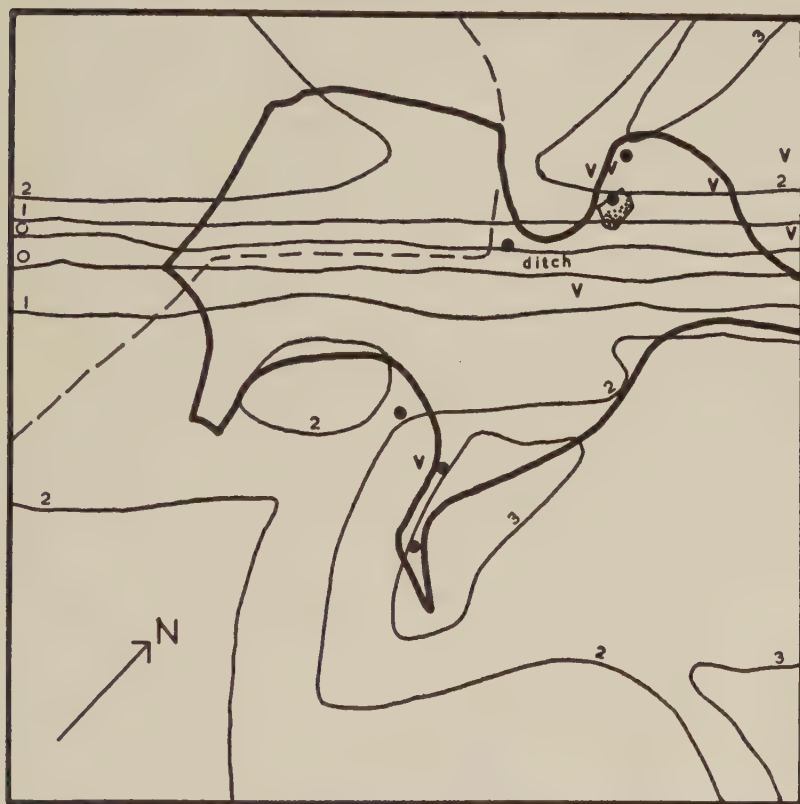


FIG. 2.— The pine-spruce glade, four years later; as figure 1 with dense bracken margin indicated by broken line.

acervorum having vanished altogether. This gives a gross density of 0.43 per m² or if the bracken (6.1 m² in area) is counted as canopy (and it has been shown to reduce insolation more than pine plantation) this figure must be increased to 0.62 nests per m². Thus even allowing for the uncertainty of the tree shadow effect (for the trees being higher would shade more of the noncanopy area after four years than before, so that the canopied zones are not quite insolationally equivalent) this density may be taken to be much less than the initial figure, that is, the nests have not been condensed (they are able under some circumstances, to move) but eliminated. The single *fusca* nest persisted (the assumption of identity

is not of course strictly permissible, but of a high degree of probability bearing in mind their specific nature and the great distance, 50 m, of other nests as well as the fact that there was a *fusca* nest in the same position in each of the three years between censuses), but it was much smaller with smaller workers and it had no sexual brood. Probably as a result of this regression it had been forced to share the stone with the *scabrinodis* colony (an inversion of the general dominance series—BRIAN 1952). The *Myrmicae* were substantially reduced: outside the canopy projection but very near to it were 4 *rubra* and 1 *scabrinodis* nests, and of the 13 *Myrmicae* in all only two were of medium size (with male pupae) the rest being small with distinctly small workers and thus like the *fusca* infertile. Although the general density was less, the highest density was greater than before: on the area of grazed grass by the stone already noted (area about 0.5 m²), there were five nests, 1 *fusca*, 2 *rubra*, 2 *scabrinodis*, all distinct as far as could be ascertained by the standard laboratory test. Such restricted concentrations are frequent (on tree stumps for example) and tend to show a characteristic zonation of species (BRIAN 1952) which may be noted in this case, too.

Thus to summarise, the tree encroachment has affected all species alike as far as can be seen. Rather than a general condensation into the area remaining suitable, there has been elimination and ultimate lower density (in terms of colonies) with a limited local concentration into the best area. Elimination probably proceeded via a deterioration in quality or vigour in the sense already considered. The biomass of FORMICIDAE must have been substantially reduced.

It has been assumed that the colonies are individually the same. The high probability of this has been indicated for the one *fusca* nest and in general this is likely to apply to the others as well. Additional colonies would have to come in through a belt of at least 50 m of uninhabitable woodland unless as foundress queens. It is not likely that queens would succeed in building colonies under conditions that must (if this alternative hypothesis is to be accepted) have caused the death of most earlier colonies. Moreover it is known that workers are not likely to live for more than four years (BRIAN 1951) and hence the original workers would probably have died and been replaced by the smaller ones. Thus all known factors favour the interpretation of the change as an elimination through a period of deterioration.

POPULATION LIMITATION

The above considerations indicate that there is no such thing as a threshold of a physical factor below which a species cannot exist and above which it can exist. There is on the contrary a variably wide transition zone in which the species varies in density and quality. The optimal combination of conditions favouring ants of this type has been listed

elsewhere and needs no repetition (BRIAN 1952). It is in such refuges that the ants are relatively free from destruction by the various influences that exist in various space-time patterns of intensity outside: mechanical disturbance of the soil, heavy trampling, watery submergence, shading out, and so on.

Within the refuge the population rises to a point where intra-and inter-species spacing and competition or shortage of food prevents further growth (for predators only occur sporadically—*Bufo bufo* occasionally, and, very rarely, *Dryobates major*). Inter-species competition with resultant partial segregation in such areas has already been discussed (BRIAN 1952, 1955, 1956) and the more general aspects of density may now be considered.

MAXIMAL NEST DENSITY

When these ideal habitats are mosaics of bare or lichen covered substratum (soil, wood, etc.) and herb growth, the nests are concentrated in the bare areas. The density of these nests may reasonably be expressed in terms of the apparently suitable area for nesting, that is in terms of the area of bare sub-strata. Thus in the small patches of lichen-covered peaty soil and regenerating heather moor which are surrounded by *Calluna vulgaris*, the areas per nest have been given (BRIAN and BRIAN 1951, Table 12) as 1.57 sq. ft. (6.85 nests per m^2) in 7—8 years old subseral vegetation and as 1.52 sq. ft. (7.08 nests per m^2) in 11—12 years old stages. A maximum density of 1.5 sq. ft. per nest (7.18 nests per m^2) is clearly indicated. This in fact represents considerable proximity for most nests will occupy very nearly a square foot (roughly 0.1 m^2) in themselves.

In the spruce—pine glade earlier considered the patch of grass by the central zone of area 6 sq.ft. (0.56 m^2) contained five nests giving 1.2 sq.ft. per nest (8.97 nests per m^2) a higher value which may perhaps be accounted for by the small size of the nests concerned. As a further example the community whose foraging has been described (BRIAN 1955 Fig. 2) may be taken. On and around stump A, as it was called, there, were 6 *rubra*, 2 *scabrinodis* and 1 *fusca* nests within an area considered suitable for nesting of 18 sq.ft. per nest (5.38 nests per m^2). Thus in general one may take a figure of 1—2 sq.ft. per nest (5-11 nests per m^2) as the maximum nest density shown by this group of species.

The question then arises as to whether such densities can be maintained over large areas, whether they are economic densities, to use Elton's term (ELTON 1932). The answer is almost certainly no for such nest-suitable areas are almost devoid of food supply. But to find relatively homogeneous areas in which nest and food sites are thoroughly interspersed and that are large enough for analysis is not easy. In fact, only two such are known throughout the locality. The first of these has been described in an other paper (BRIAN 1956) and consists of a rectangular patch of

heather in acidic grassland occupied entirely by *M. scabrinodis*. It had an area of 1 m² and contained 77 nests giving a density of 0.70 nests per m². The second is a square of side 10 yards (9.41 m), a permanent quadrat in rabbit grazed plagioclimax developed from felled woodland subseres, an ecosystem that has been described in some detail before (BRIAN 1952, pp. 12-14). At its maximum ant density (in 1949) this quadrat (which will be reported fully after some more years of observation) contained 58 nests of all four species giving a nest density of 0.69 per m². These two figures thus agree closely even though they are derived in one case from a single species population and in the other from a 4-species population and even though the ecosystems themselves differ, they may be taken as a provisional estimate of the maximum economic density.

NEST DISTRIBUTION

Are these densities controlled by interactions within the populations? One of the customary methods of investigating this is to consider the mode of the dispersion of the nests: either over-dispersion or a minimum distance apart of greater frequency than that expected on a random basis indicates that intrinsic factors are affecting the spacing. On the other hand the absence of these may not be taken as negative evidence for nest site potentiality may itself be a random variable and it has already been shown that considerable nest proximity can be tolerated.

In an earlier paper (BRIAN 1952 p. 14) stump and off-stump populations in a plagioclimax developed from felled woodland were compared by considering as pairs of samples 30 stumps and 30 sq. yd. quadrats (taken

TABLE 1. — ANALYSIS OF SAMPLES TAKEN IN PLAGIO-CLIMAX ON STUMPS AND BETWEEN STUMPS (DATA FROM BRIAN 1952, PAGE 14).

NUMBER of nests	ON STUMPS		BETWEEN STUMPS	
	Observed	Poisson	Observed	Poisson
0	0	3.68	7	9.99
1	10	7.73	15	10.99
2	11	8.12	6	6.04
3	6	5.68	2	2.22
4	3	2.98	0	0.76
5 and over	0	1.81		
Probability of				
Poisson fit	0.1-0.2	0.2-0.3	
Index of dispersion	13.6	19.1	
Probability				
of above (29 df)	< 0.01	0.05-0.1	

in the ant inhabited area near each stump). At the time, although the possibility of over-dispersion was noted it was thought that the data was insufficient for statistical analysis. Now following the advice of COCHRAN (1954) the data has been reconsidered (Table 1). Both sets of data depart appreciably from the Poisson distribution especially the stump set although even this does not achieve statistical significance. However, the index of dispersion has a value (on stumps) 13.6 and (off stumps) 19.1, both these figures considerably less than the number of degrees of freedom (29) that are available, but only the first clearly significant ($P < 0.01$). Bearing in mind that stumps vary in size and shape somewhat there does appear good evidence for supposing that they have a limited capacity for ants' nests, in the order of one or two.

The permanent quadrat in this same type of habitat, to which reference has already been made, was analysed in this way (also at its maximum population in 1949). The area was divided into 36 squares each of side 5 ft., and the numbers per square observed and expected (Poisson) have been tabulated (Table 2) for all four species together and for the

TABLE 2. — ANALYSIS OF SPECIES DISTRIBUTION IN A PERMANENT QUADRAT IN PLAGIOCLIMAX.

NUMBER of nests	ALL 4 SPECIES		M. RUBRA		M. SCABRINODIS		L. ACERVORUM	
	Observed	Poisson	Observed	Poisson	Observed	Poisson	Observed	Poisson
0	11	7.20	13	15.70	23	23.65	28	27.21
1	9	11.59	16	13.03	11	9.93	6	7.62
2	7	9.33	7	5.41	2	2.09	2	1.07
3	4	5.01	0	1.50				
4	3	2.01						
5	1	0.65						
6	1	0.17						
Probability of								
Poisson fit...	0.1-0.2	0.1-0.2	0.5-0.7	0.3-0.5	
Index of								
dispersion ...	53.76	22.89	30.36	40.07	
Probability of								
above (35 df).	.001-.01073128	

three most abundant separately. For all species together there are more empty squares than expected and more with four or over nests than expected but less with 1, 2 and 3, a sign of aggregation. This does not attain statistical significance when the deviations from Poisson alone are considered but the index of dispersion is so large and its probability so small that the reality of aggregation need not be doubted. This result is contrary to what might be expected but is clarified when the individual species are considered.

The most numerous of these (*M. rubra*) gave less empty squares than expected but more with 1 or 2 nests. This distribution does not differ significantly from that of the Poisson, but the index of dispersion, 22.89, is very much smaller than the number of degrees of freedom (35) and has a probability of only 0.07. The distributions of *M. scabrinodis* and of *L. acervorum* are very nearly random, the former having an index less than and the latter more than the number of degrees of freedom. The fourth species, *F. fusca* existed as three nests, one on each of the three stumps that were well spaced apart.

Thus a grouped distribution which tends to aggregation is generated in spite of individual distributions that are random or tend to be over dispersed. Evidently intraspecies avoidance of some intensity, perhaps only mild is accompanied by interspecies attraction but this is unlikely as far as general observation suggests; on the other hand, the fact that nest-suitable terrain is patchy is undoubted.

A tendency to a minimal distance between nests has been noted by TALBOT (1943) for the ant *Prenolepis imparis* Say. Using the spacing method suggested by SKELLAM (1952) and elaborated by MOORE (1954) and working from her diagram, it can be shown that small distances are less frequent and slightly larger ones more frequent than would be expected if the nests were randomly distributed ($P < 0.001$). TALBOT (1954) has suggested that the nests of *Aphaenogaster traetae* FOREL are also over-dispersed; using the same method it can be shown that the smallest distances are less and the medium distances more frequent than would be expected on a random basis ($P < 0.001$). Hence over-dispersion of colonies is characteristic of at least three species of ground nesting ant.

QUEEN CONDENSATION

One of the ways in which intraspecies dispersion and interspecies aggregation can develop is through queen condensation. The foundress queens settling in newly colonised terrain may associate in monospecific groups (primary pleometrosis) and these may either only remain open until workers appear or they may continue to accept queens (secondary pleometrosis) but in both cases the distribution of colonies may be expected to tend towards over-dispersion if the uniformity of the environment permits. In the former case, the life span and reproductive capacity of the colony is predetermined; in the latter, unlimited. Secondary pleometrosis appears to be particularly useful to colonies that occupy persistent feeding areas in stable ecosystems and that can expand and impose themselves on neighbouring species and colonies. But in the community of SCOTTISH ants it seems restricted to the form *microgyna* of *M. rubra* (BRIAN and BRIAN 1949) and to the sparse *L. acervorum* (DONISTHORPE 1927) only the latter of which is present in the mixed communities considered here (*microgyna* occurs in isolated patches in

hedgerows, etc.). The primary pleometrosis of *M. rubra macrogyna* does not seem to lead to groups of more than four queens very often (BRIAN and BRIAN 1949, Table 5; BRIAN 1952, Fig. 2) even in optimal concentration sites. Frequently two small young colonies of this species were found in a single tree stump (BRIAN and BRIAN 1951, Table 13). Donisthorpe's (1927) summary of the literature indicates that *F. fusca* is strongly primarily

TABLE 3. — THE NUMBER OF QUEENS IN COLONY-FOUNDING GROUPS OF 3 SPECIES.

SPECIES	NUMBER IN GROUP											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>F. fusca</i>	1	4	2	—	—	—	—	—	—	—	—	1
<i>M. rubra</i>	2	2	1	1	—	—	—	—	—	1	—	—
<i>M. scabrinodis</i> ...	1	1	—	—	—	—	—	—	—	—	—	—

pleometrotic. The following table (Table 3) shows the number of queens in groups of three of the species that resulted from a collection made in the vicinity of this study.

TERRITORIAL BEHAVIOUR

A further factor favouring over-dispersion is territorial behaviour. DONISTHROPE (1927) has collected substantial evidence from the work of FOREL, LUBBOCK and CRAWLEY to show that strange queens of *fusca* are killed by workers even under natural conditions when running past nests of their own species (FOREL). The territorial status of the species of this community has been considered elsewhere (BRIAN 1955) and appears quite adequate to enable queens either to be harried continually and prevented from settling down or to be destroyed in some stage of colony foundation. Of especial interest is the fact that evidence was given to show how intraspecies actions could be more intense than interspecies action; whereas workers could detect a different species at a short distance, presumably chemically, it was necessary for contact to be made for an intercolonial intraspecies discrimination; and this greatly increased the chance of either lethal grappling or if a secure and special grip was obtained, of being carried to the hostile nest and destroyed.

THE INCIDENCE OF QUEEN FOUNDRESSES

From these observations one would expect far more queens to start colonies in newly available areas than in populated ones. With a view to testing this, a woodland was discovered that had been felled 15 years

prior to the present study and in which three areas with different types of vegetation caused by differences in management existed very close together (within a 70 m square). One part had been left after felling and had developed into the typical rabbit grazed heath grassland plagioclimax so often discussed in this series; this contained a dense four-species population of ants based largely on the old stumps. A second part had been closely planted with pines which had grown to nearly close the canopy and contained only a few small colonies of *M. rubra*. A third had been similarly planted and allowed to grow until the previous year when it had been clear felled; it likewise contained only a few small colonies of *M. rubra*, as time had not been adequate for recolonisation.

TABLE 4. — SPECIES AND HABITAT ANALYSIS OF THE FOUNDRESS QUEENS FOUND IN 10 STUMPS.

HABITAT	<i>Fusca</i>	<i>Rubra</i>	<i>Scabrinodis</i>	TOTAL
Plagioclimax	5	1	2	8
Pine plantation . . .	—	7	—	7
Felled pine plantation	22	15	1	38

Ten stumps were carefully examined in each area and the queens noted in each. This was done in March when heat orientation is likely to be maximal and the queens fully settled in cells for foundation. Results are summarised in Table 4. All habitats yielded ant queens but the freshly exposed one had by far the most—over four times as many as the others. The plagioclimax yielded all species in small numbers as did the felled pine plantation, but the standing pine plantation yielded only *rubra*. This is perhaps because *rubra* are less strongly attracted by light-reflecting surfaces and by warmth. The difference in density between the plagioclimax and the freshly exposed area may of course also be due to habitat selection behaviour for it is quite possible that the fully exposed area was brighter and more attractive to the flying queens. Nevertheless, it is likely, though unproven, that their habitat selection after casting their wings (on alighting) is influenced by population density, registered perhaps as hostile contact frequency (compare the great tit results of KLUYVER and TINBERGEN 1953 and the ant-lion results of MORISITA 1952).

The account of populations in subseres (BRIAN and BRIAN 1951) supports these claims for it was shown that at first small colonies and then large ones predominated (although a few queens appeared even with the large colonies). That is, the areas are occupied in a relatively short period after which the colonies grow with little addition to their numbers. Also it has been noted before (BRIAN 1952) that in plagioclimax of the type discussed, nests were large as a rule and only a few queen foundresses were found.

TALBOT (1943) thought that the queens of *Prenolepis imparis* Say. founded nests randomly. There was a great excess of them in the orchard studied. Many were predated and many seemed to die of unsatisfactory conditions in their places of settlement. She argued that the orchard was by no means saturated with ants but this is difficult to ascertain without experiments. It would seem that in certain regions maximal densities must have developed on account of the spacing distribution already mentioned; these the queens would probably avoid or be driven away from to attempt foundation in less suitable places if they escaped being eaten by predators in transit.

DISCUSSION

Thus considerable evidence exists in favour of the view that population density is limited in favourable habitats by intraspecific and interspecific competition. The former leads to a spacing of the nests of a species throughout a range of habitat variation which is determined by the latter. Interspecific competition thus causes species segregation (as well as different behaviour and requirements) as has been fully discussed elsewhere (BRIAN 1952, 1955, 1956) and presses the ant population out so that the maximum suitable area is inhabited. To discover how efficiently the resources are used under these conditions is clearly the next step in analysis.

The general facts of population limitation that apply to this group of ants harmonise quite well with the theory of THOMPSON (1929, 1939) and perhaps even better with that of SOLOMON (1949) which gives a greater emphasis to the ecosystem. The ants occur in seral vegetation as transient inhabitants and in biotic plagioclimaxes of certain sorts as permanent residents. In the seral vegetation they are limited to the insolation-high spots of lichen-covered soil and may in these reach self limited densities. But it is quite likely that sometimes they may fail to attain such levels and one may then obtain a situation such as ANDREWARTHA and BIRCH (1954) have emphasized—that of a population destroyed by environmental action long before it reaches a density high enough for self-regulation.

In those cases where mammals and grasses enter to create a stable ecosystem, this, especially if hot, thin, fairly moist and not liable to mechanical damage by the grazing animal, causes the ant population to build up to a self-limited value which is probably a function of the food supply, but this needs more investigation. This appears to be the limiting state which NICHOLSON (1954) has emphasised. Under these circumstance the species composition is related principally to the nest-site type and availability.

Of the two principle requirements which ants have: nest-site and food-supply, it is quite obvious that the former is more generally limiting when the area as a whole is considered. This comprises a wide variety of habitats ranging from the coastal areas along the FIRTH of CLYDE or

LOCH LOMOND up through agricultural land and rough grazing to heather moor. In most of these, some sort of insect prey and some sort of Homoptera to give plant juices are available—and these ants are remarkably catholic in their tastes. But few habitats provide, hot, windless, humid, mechanically resistant, rain impervious sites for nesting in nearly sufficient proportion. One exception to this, the transient early stage of subseres, provides little or no food supply but this seems to regenerate with herb growth quickly enough to out-pace any population growth. The other exception, plagioclimax grazed by light animals, is rare.

In the food rich areas that are devoid of nest-sites quick increases in population can be obtained by distributing and fixing slabs of stone or slates and this may be successful even in the more permanent pastures grazed by cattle. It clearly remains to discover what is the optimum nest density and food supply, not forgetting that territorial behaviour which is probably a function of the latter, is likely to be the governing factor in the population at maximal density.

Summary.

1. An account has been given of the changes that accompanied the gradual overgrowth of a glade in Spruce-Pine woodland. Although some small scale condensation into favourable nest-sites occurred, the general process was one of colony elimination and a reduction in mean nest density.

2. The maximal nest density was of the order of 5 to 11 nests per m^2 and the maximum economic density was 0.7 nests per m^2 . Whereas in a quadrat the 4-species population was aggregated, each species considered alone was either randomly distributed or overdispersed. No doubt this resulted from intra-species avoidance combined with interspecies indifference in a heterogeneous habitat and some relevant behaviour traits are considered.

3. In general, the abundance of ants in the area is limited by lack of suitable nest sites.

Résumen.

1. Se ha tratado sobre los cambios que acompañan el crecimiento paulatino de yuyos sobre un claro dentro de un bosque de pinos y abetos. Auncuando ocurrió en pequeña escala una condensación favorable para el sitio de nidos, el proceso en general fué de eliminación de colonias y reducción de la densidad de nidos.

2. La densidad máxima de nidos fué de 5 à 11 nidos por m^2 y la máxima densidad económica de 0.7 nidos por m^2 . Mientras que en un cuadrado fué agregada la población de las cuatro especies, considerandola por separado, cada especie fué distribuida al azar o esparcida demasiadamente.

Esto, sin duda, resulta de la costumbre de las especies de evadirse junto con la indiferencia de las mismas dentro de una habitación heterogénea y se consideran también rasgos de conducta pertinentes.

3. En general, la abundancia de hormigas en el area se ve limitada por la escasez de sitios ideales para nidos.

REFERENCES.

1954. ANDREWARTHA (H. G.), BIRCH (L. C.). — The distribution and abundance of animals. Chicago University Press.
1949. BRIAN (M. V.), BRIAN (A. D.). — Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nyl (*Trans. R. ent. Soc. Lond.*, **100**, 393-409). — 1951. Insolation and ant population in the West of Scotland (*Trans. R. ent. Soc. Lond.*, **102**, 303-330).
1951. BRIAN (M. V.). — Summer population changes in colonies of the ant *Myrmica*. (*Physiologia Comparata et Oecologia*, **2**, 248-262). — 1952. The structure of a dense natural ant population (*J. Anim. Ecol.*, **21**, 12-24). — 1955. Food collection by a Scottish ant community (*J. Anim. Ecol.*, **24**, 336-351). — 1956. Segregation of species of the ant genus *Myrmica* (*J. Anim. Ecol.*) (in press).
1954. COCHRAN (W. G.). — Some methods for strengthening the common χ^2 tests (*Biometrics*, **10**, 417-451).
1927. DONISTHORPE (H. J.). — British ants. London.
1932. ELTON (C. R.). — Orientation of the nests of *Formica truncorum* F. in North Norway (*J. Anim. Ecol.*, **1**, 192-193).
1953. KLUYVER (H. N.), TINBERGER (L.). — Territory and the regulation of density in Titmice (*Arch. Neder. Zool.*, **10**, 265-289).
1954. MOORE (P. G.). — Spacing in plant populations (*Ecology*, **35**, 222-227).
1952. MORISITA (M.). — Habitat preference and the evaluation of the environment of an animal. Experimental studies on the population density of an ant-lion *Glenurodes japonicus* ML (*Jap. J. Physiol. Ecol.*, **5**, 1-16).
1954. NICHOLSON (A. J.). — Compensatory reactions of populations to stresses and their evolutionary significance (*Aust. J. Zool.*, **2**, 1-65).
1948. RAINIER (A.). — L'économie thermique d'une colonie polycalique de la Fourmi des bois (*La Cellule*, **51**, 281-368).
1952. SKELLAM (J. G.). — Studies in statistical ecology, 1. Spatial pattern (*Biometrika*, **39**, 346-362).
1949. SOLOMON (M. E.). — The natural control of animal populations (*J. Anim. Ecol.*, **18**, 1-35).
1947. STEINER (A.). — Der Wärmehaushalt der einheimischen sozialen Hautflügler (*Schweiz. bienen Ztg.*, **2**, 139-256).
1943. TALBOT (M.). — Population studies of the ant *Prenolepis imparis* Say (*Ecology*, **24**, 31-44). — 1954. Populations of the ant *Aphaenogaster* (*Attomyrma*) *traetae* Forel, on abandoned fields on the Edwin S. George reserve (*Contributions from the Laboratory of Vertebrate Biology, University of Michigan*, number, **69**, 9 pp).
1929. THOMPSON (W. R.). — On natural control (*Parasitology*, **21**, 269-281). — 1939. Biological control and the theories of the interactions of populations. (*Parasitology*, **31**, 299-388).
1953. WAY (M. J.). — The relationship between certain ant species with particular reference to biological control of the Coreid, Theraptus sp. (*Bull. ent. Res.*, **44**, 669-691).
1954. YARROW (I. H. H.). — The British ants allied to *Formica fusca* L. (Hym. Formicidae) (*Trans. Soc. Brit. Ent.*, **11**, 229-244). — 1955. The type species of the ant genus *Myrmica* Latreille (*Proc. R. ent. Soc. Lond.*, **24**, 113-115).

NOTES ON THE ANT GENUS *HOLCOPONERA* MAYR, WITH DESCRIPTIONS OF TWO NEW SPECIES

by

WILLIAM L. BROWN, Jr.

(*Museum of Comparative Zoology, Harvard University*).

In another place, I am offering as soon as possible a generic revision of tribe Ectatommini (subfamily Ponerinae). In the manuscript of this revision, I have been able to revise to species level, or at least give keys to the valid species of, several of the genera treated. Certain of the genera, however, proved too large and presented too many difficulties in the way of type procurement to be handled in this way. The revisionary notes that were gathered on at least a few of the species in such genera are scarcely more than by-products of the larger work, and it is felt that they are better published separately so as to cut down the bulk of the generic revision to a more useful size.

One of the genera that proved most difficult at species level was *Holcoponera* Mayr. This genus has already undergone one revision by Santschi (1929, Zool. Anz., 82: 437-477, 47 figs.), who described a great many species and infraspecific variants in the pentanomial system of nomenclature. Santschi's paper at least has the virtue of having brought together scattered types and descriptive material, and the drawings are useful. It is unfortunately true, however, that his treatment lacks the consistency necessary for interpretation of his taxonomic actions in the light of modern population systematics. In *Holcoponera*, Santschi seized upon almost any difference, however minor, to serve as the basis for a new name. Especially singled out were such "diagnostic" characters as the mesepisternal lobe or flange, density of the costulate sculpture, form of the petiole and subpetiolar process, overall body size and proportions of the antennal segments—all characters showing a wide range of variation in *Holcoponera*. Apparently little effort was made to determine how this variation was limited, if at all, in single populations or even in single nest series, so that Santschi saw no inconsistency in describing from La Palma, 1600 M., Costa Rica, the form *H. simplex foreli* in mixture with other workers that he himself determined as *H. simplex simplex*, despite that fact that Forel had described the exceedingly similar *H. satzgeri* earlier from precisely the same locality!

Santschi had two methods of dealing with intergrades between the forms he recognized as nameworthy: he either ignored these intermediates, or he named them as subspecies or varieties. The most unfortunate result of such a practice is that the true species limits are obscured by a maze of poorly-characterized forms that cannot be traced to their correct species without a review of type material—a review taking more time and trouble than I care to spend at present. I shall therefore satisfy myself for now by dealing only with a few obvious and uncomplicated synonymies, which at least will balance for the future reviser the additions I am making here to the genus of two new species and one new combination. These additions are made because they are of more than routine interest in extending our conception of the amount of radiation that has occurred within *Holcoponera*.

Holcoponera striatula Mayr.

Gnamptogenys striatula Mayr, 1883, *Hor. Soc. Ent. Ross.*, 18 : 32, worker.

Type locality : French Guiana.

Holcoponera striatula var. *antillana* Santschi, 1929, *op. cit.*, p. 444, figs.

16, 21, worker, male. Type locality : Martinique. New Synonymy.

The characters cited by SANTSCHI are insignificant and show all degrees of intergradation in several series I have seen from Jamaica and elsewhere in tropical America. The Jamaican series alone will serve to illustrate this variation perfectly. Undoubtedly several other forms in the *striatula-brasiliensis* complex will fall as synonyms of *striatula* when the types and additional material can be studied. A large and varied lot of specimens belonging to this complex is in the collections of the U. S. National Museum and the Museum of Comparative Zoology, and I mention this here because these series will be invaluable to the eventual reviser of the group.

Holcoponera simplex Emery.

Ectatomma (Holcoponera) simplex Emery, 1896, *Bull. Soc. Ent. Ital.*, 28 : 46, fig. 7, worker, female. Type locality : Alajuela, Costa Rica.

Ectatomma (Holcoponera) Satzgeri Forel, 1908, *Bull. Soc. Vaud. Sci. Nat.* 44: 39, worker. Type locality: La Palma, 1600 M., Costa Rica. New Synonymy.

Ectatomma (Holcoponera) simplex subsp. *spurium* Forel, 1908, *ibid.*, p. 39, worker. Type locality: 'Guatemala (received from M. PERGANDE).' New Synonymy.

Holcoponera simplex st. *foreli* Santschi, 1929, *op. cit.*, p. 460, fig. 34, worker. Type locality: La Palma, 1600 M., Costa Rica. New Synonymy.

In his 1929 work (pp. 459-462, fig. 33-37), SANTSCHI discusses all of these synonyms with illustrations, and cites further references (among which there are several errors in transcription of names, dates, etc.). In my introductory remarks, above, I have already referred to Santschi's recognition of the three conspecific variants at one locality and possibly, at least in part, from the same nest series. The differences supposed to separate these forms appear from Santschi's own paper to be trivial individual variations, paralleled in single series available to me from La Carpentera, Costa Rica (W. M. MANN) and from Hamburg Farm, Santa Clara Prov., Costa Rica (F. NEVERMANN). The name *spurium* applies to a single worker distinguished by similarly unreliable features, and supposedly from Guatemala. However, some or all of Pergande's material labelled as "Guatemala" may actually have come from Costa Rica, judging from the list of other ant species mentioned by Forel in various papers in which he dealt with this particular batch. Whether or not the locality cited is the correct one, however, the grounds for its distinction

by name from *H. simplex* are unconvincing, and it seems better for the present to consider *simplex* as a single distinct and rather localized species, easily recognized by the predominantly transverse costation of its post-petiolear sternum.

Holcoponera relictæ (MANN) new combination.

Rhopalopone relictæ Mann, 1916, *Bull. Mus. Comp. Zool.*, 60: 403, pl. 1, fig. 4, 5, worker.

The species *relictæ* is referred to *Holcoponera* only after the discovery of the closely related *Holcoponera mina*, described below. *H. mina*, as will be seen from the description and then the discussion, is exactly intermediate between *relictæ* and the remainder of the *Holcoponera* species, as represented by *H. strigata* (NORTON).

DESCRIPTIONS OF NEW SPECIES

The measurements and proportions are cited with abbreviations, the key to which is as follows: TL, total outstretched length, including mandibles; HL, full length of head with clypeus, excluding mandibles; HW, width of head across eyes; WL, diagonal length of alitrunk as measured from side view; CI, cephalic index, or width of head expressed as a percentage of HL ($HW/HL \times 100$).

Types are deposited in the United States National Museum, which owns the holotypes and a first set of paratypes; paratypes of each species are in the Museum of Comparative Zoology at Harvard University. I wish to thank Dr. M. R. SMITH, of the National Museum, and Dr. F. БРЯК, of the Naturhistoriska Riksmuseet, Stockholm, for their aid in loaning specimens.

Holcoponera acuta new species (fig. 1).

Holotype worker: TL 4.7, HL 1.04, HW 0.90, WL 1.45 mm.; CI 87. Greatest diameter of compound eye about 0.20 mm. Exposed scape L 1.00 mm. (TL does not include the downcurved apical segments of the gaster.)

Color deep reddish brown, appendages and mandibles yellowish ferruginous. Costulation of medium density and coarseness, shining and with shining interspaces, approximately 30 (28-31) costulae between the compound eyes, 9 between the posterior extremities of the frontal carinae, 10 or 11 on the mesepisternum. Costulation transverse on the extreme anterior pronotum, the alitrunk otherwise longitudinally costulate. Petiolear node seen from above with concentric costulation around a few median

longitudinal elements (more regularly circular-concentric in some paratypes). Postpetiole and succeeding segment longitudinally costulate, the latter a bit more finely so; exposed tergital strip of second postpetiolar segment transversely striate in the middle, the striation becoming oblique laterad.

Head of the usual *Holcaponera* form; occipital border seen in perfect full-face view approximately straight, with a slight tendency toward concavity in the middle; posterolateral lobes moderately developed, slightly protruding beyond occipital border in full-face view and rather narrowly rounded as seen from the side (better developed than in *H. striatula* Mayr, but not so strongly as in *H. curtula* Forel, and not subtruncate). Eyes large, convex, their centers situated precisely at the posterior third of the head length (HL). Antennal scapes extending beyond occipital border by about 28% of their total exposed lengths. All segments of funiculus longer than broad, but segments 3-10 only slightly so.

Alitrunk of the form usual in the more slender *Holcaponera* species; propodeum with a definite, but obtuse and somewhat rounded margin setting off the declivity on the sides and above; dorsum of propodeum above with a very shallow transverse impression. Mesepisternal lobe (the mesosternal lobe of Santschi) reduced to a low anterior remnant with rounded border lying over the anterior coxa, and, after a brief gap, a low median tooth or tubercle.

Petiole (fig. 1) highly distinctive, its node inclined posteriad and its



Fig. 1. — *Holcaponera acuta* Brown, paratype worker.

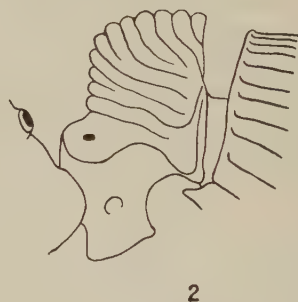


Fig. 2. — *Holcaponera mina* Brown, paratype worker. Left side views of petiole and neighboring structures.

upper portion produced posteriad as a distinct, subconical, dorsoventrally flattened tooth, resembling the condition seen in *Heteroponera dolo* (ROGER), *Rhytidoponera reticulata* Forel and *R. acanthoponeroides* Vieh-meyer to varying degrees. From dorsal view, the posterapical process is less acute, but still quite distinct and normally overhanging the surface of the postpetiolar segment. Subpetiolar process as shown in the figure; triangular, terminating in a rounded tooth curved posteriad. Postpetiole

without a well-defined anterior face, the striation continuing around the convex anterior portion without interruption almost to the anterior articular ring. Tooth on hind coxa small but acute.

Pilosity fine, tapered, sparse over dorsal surfaces of body, where the few longer hairs (average L ca. 0.28 mm.) appear to be arranged in bilateral symmetry. Shorter inclined and reclinate hairs sparse over appendages and arranged in sparse tufts along the posterior borders of the gastric segments on each side of the midline; exposed surfaces of ventral and dorsal segments at gastric apex each with a dense tuft or brush. Pubescence moderately abundant on appendages, mostly more or less reclinate.

Paratype workers (12 specimens from same nest as holotype), vary from about the size of the holotype up to specimens with a TL of 5.0 mm. and HL 1.14 mm. The head width varies slightly (CI 86-90), and the number of costulae between the compound eyes varies from about 26 to 31. The shape of the mesepisternal lobe is extremely variable; in a majority of specimens, the lobe forms a single convex flange extending nearly the entire length of the ventral border of the mesepisternum; in others, the lobe is reduced to a small irregular triangular flap overlapping the posterior part of the fore coxa. The lobes on opposites sides of the same specimen may differ considerably. There is some slight variation in the scape length, strength of the dorsal transverse impression of the propodeum, and in the form of the subpetiolar process.

Female (dealate). — TL 5.6, HL 1.18, HW 1.06, WL 1.82 mm., CI 90; greatest diameter of eye about 0.26 mm., exposed scape L 1.06 mm. Petiolar node slightly higher and slightly more compressed in an anterior-posterior direction relative to the situation in the worker, tooth at apex of node slightly inclined dorsad from the horizontal. Subpetiolar process with the sloping posterior border at midlength furnished with a low, obtusely rounded suggestion of a posteroventral lobe. Three ocelli present, moderate in size; 31 costulae between compound eyes. Median segments of funiculi almost or quite as broad as long, depending on angle of view. Otherwise differing from the worker by the characters usual for the genus.

Male. — Similar to the males of *H. striatula* Mayr, *H. curtula* Forel and *H. Wheeleri* Santschi in size, form and venation of forewing, but differing markedly in sculpture. Dorsum of head, including, clypeus, striate, weakly shining; posterior alitrunk with indistinct traces of striation, otherwise smooth and shining; mandibles with coarse longitudinal punctures; petiole and succeeding tergite shining, almost smooth, with feeble and loosely coriaceous surface. Body otherwise smooth, shining, with scattered punctures, becoming dense on appendages. Pilosity much as described for worker, the longer hairs not as long as in worker. Color piceous; appendages ferruginous; wings clearer than in *H. striatula*. The subpetiolar appendage terminates in a slender tooth, directed antero-

ventrad, instead of the bulky lobe of *striatula*. Compound eyes elongate-subreniform, convex, greatest diameter 0.38 mm., or slightly greater than the exposed length of a mandible measured from base to apex (slightly larger than in *stritula*). Gastric apex with genitalia missing.

The type series consists of the holotype worker, 12 paratype workers, one male and one female paratypes, collected by Dr. W. M. MANN at Huachi, Beni, Bolivia, during September, 1922. Though two kinds of labels are found on the various pins, all appear to represent the same nest series. This highly aberrant species is related to the group about *H. porcata* Emery. It can easily be recognized in the worker-female castes by means of the dentiform petiolar apex.

Holcoponera mina new species (fig. 2).

Holotype worker: TL 3.2, HL 0.73, HW 0.64, WL 1.00 mm.; CI 88. Greatest diameter of compound eye slightly less than 0.09 mm. Exposed L scape 0.54 mm. 22 distinct costulae between compound eyes; mesanepisternum with one oblique costa between the upper and lower costiform borders of the sclerite; mesokatepisternum with 5 short longitudinal costae between upper and lower costiform borders, making 10 costae total for each mesepisternum. Costation otherwise also rather coarse (relative to body size); 5-6 transverse costae on anterior pronotum; alitrunk otherwise, including propodeal declivity, predominantly longitudinally costate. Gaster longitudinally costate, sternum of post-petiole prevailingly so; sternum of succeeding segment transversely striate; exposed surfaces of apical gastric segments largely smooth, shining. Petiolar node transversely costate in front and above, the costae continuing obliquely posteroventrad on the sides (fig. 2). Mandibles and appendages with fine punctulation, largely more or less shining.

Pilosity moderate in length, fine, mostly inclined, fairly abundant and generally distributed except on appendages, forming sparse tufts or brushes on apical gastric segments. Pubescence fine, short, dense, reclinate, largely confined to appendages and mandibles. Clypeus with 4 long, fine hairs. Color (holotype is probably not at absolutely full adult coloration) medium-light reddish brown, mandibles, legs and antennae yellowish.

Head with parallel, feebly convex sides, occipital border virtually straight, with the merest hint of concavity as seen in perfect full-face view. No occipital lobes developed. Eyes small, with 7-8 facets in greatest diameter, their anterior margins precisely at the midlength of the head (mid-HL). Scares short, gently curved at base and incrassate apicad, just barely overreaching occipital border as seen in perfect full-face view. Funiculus incrassate apicad, the last three segments forming a fairly distinct clava, although the two segments preceding the last three might also be included, to make a 5-segmented clava.

Alitrunk compact, evenly and gently convex, with only a trace of an impression on the posterior propodeal dorsum. Propodeal declivity plane, steep, set off from sides and dorsum by a distinct but obtuse angle or margin. Propodeal spiracles prominent, projecting posteriad from the lateral margins of the declivity. Mesepisternum divided by a distinct suture into upper and lower pieces; katepisternal lobe moderate in width, tapering gradually posteriad, with a gently convex free margin. Form of the petiole seen from the side as in fig. 2, as seen from above, the node is thick subdisciform, with upper surface transverse; node about $1\frac{1}{3}$ times as broad as long, with convex anterior and truncate posterior outline; costation of apex gently arched-transverse; posterior face broad, semi-circular, vertical, with loose transverse costation. Anterior face of postpetiole vertical, nearly smooth, set off sharply from the costate dorsum and sides by an irregular but continuous transverse rim or carina. Hind coxae each with a distinct but short tooth above; middle and posterior tibiae each with a single small, pectinate spur, the lateral spur, if present at all, reduced to similarity with adjacent setae, and therefore not readily identifiable; extra ("median") tooth of tarsal claw distinct, near base on all claws.

The holotype, together with 3 paratype workers (one headless) and a dealate, headless type female, were taken at Tumupasa, Bolivia (W. M. Mann *leg.*). The type nest series shows only slight variation among the workers; the color varies from light-medium to deep reddish brown, with mandibles and appendages ferruginous yellow; two specimens have slightly longer heads relatively than in the holotype, and there exist minor differences in sculpture.

Three additional workers from Llinguipata, Peru (N. HOLMGREN, Naturh. Riksmus., Stockholm) are larger (average HL 0.84 mm.), dark reddish brown in color, and tend to have the occipital outline a bit more distinctly concave. The largest of these has an extremely feeble sulciform line, traceable as a series of dents in the costae, running transversely across the posterior propodeum to mark the site of the obsolete metanotal groove; the specimen may be a worker-female intergrade.

Female. — The headless dealate from the type nest series is larger and more robust than the corresponding workers (WL 1.30 mm.). Petiolar node higher and more compressed anteroventrally than in workers, as is usual among ponerines; seen from above, the node is about twice as broad as long. Color and pilosity as in darker workers.

H. mina is the smallest *Holcoponera* so far reported as a member of the genus, and it seems to be most closely related to the two other small species: *H. strigata* Norton, found in southern Mexico southward to Honduras, and *H. relictata* Mann, from the Amazon Basin; measurements of *Holcoponera* species in the literature are usually too low. The closest relationship is with *H. relictata* (size, eye size, short scapes, tendency in some specimens to appearance of metanotal "suture," prominence of

propodeal spiracles, structure of petiole and especially of postpetiole), and *H. mina* is the intermediate form that decided for me the removal of *relicta* from *Rhopalopone* to *Holcaponera*. *H. mina* is distinguishable from *H. relicta* by a number of details, chief among which are the much thicker, less disciform petiolar node and the absence in *mina* of a distinct metanotal groove in normal workers. *H. strigata* and the other *Holcaponera* species differ in the structure of the postpetiole, which in all these species forms one continuously curved and uniformly costate convexity over the major anterodorsal surfaces.

Summary.

In *Holcaponera*, thorough revisionary work is rendered difficult by the poor quality of previous descriptions, by the excessive splitting of SANTSCHI in his revision of 1929, and by the difficulty of seeing all of the types involved. New synonymy is offered where the need is obvious in a few cases. *H. striatula* var. *antillana* Santschi proves to be an individual variant of *striatula* and is unworthy of nomenclatorial distinction. *H. simplex* Emery includes, as individual variants without claim to formal names, the three nominal species or subspecies from Costa Rica (*simplex* s. str., *satzgeri* Forel and *foreli* Santschi). Another synonym, *H. spurium* Forel, occurs doubtfully in Guatemala. The species *relicta* Mann is transferred from *Rhopalopone* to the genus *Holcaponera* because the new species *H. mina* is intergradient between it and the other *Holcaponera* species. Two new species are described: *H. mina*, from Bolivia and Peru, and *H. acuta*, from Bolivia.

Zusammenfassung.

Eine gründliche Revision von *Holcaponera* ist sehr erschwert, einmal durch frühere mangelhafte Beschreibungen, dann durch Santschis übermäßige Aufgliederung in seiner Revision von 1929, und durch die Schwierigkeit alle betreffenden Typen sehen zu können. Einige neuen Synonymen wurden festgestellt; *H. striatula* var. *antillana* Santschi ist nur eine individuelle Variante von *striatula*, und kann daher nomenclatorisch unbeachtet bleiben. *H. simplex* Emery schliesst als individuelle Varianten, ohne Anspruch auf formelle Namen, die drei sogenannten Arten oder Unterarten aus Costa Rica ein (*simplex* s. str., *satzgeri* Forel und *foreli* Santschi). Das Auftreten von die synonymische *H. spurium* Forel in Guatemala ist zweifelhaft. Die Art *relicta* Mann wurde von der Gattung *Rhopalopone* zu der Gattung *Holcaponera* überführt. Die neue Art *H. mina* verknüpft *H. relicta* mit den andern Arten dieser Gattung. Zwei Arten sind neu beschreiben: *H. mina* (Bolivien und Peru) und *H. acuta* (Bolivien).

Résumé.

Il est difficile de faire une revision complète des *Holcoponera*, à cause des mauvaises descriptions publiées jusqu'ici, du morcellement excessif introduit par SANTSCHI dans son travail de 1929 et de l'impossibilité d'examiner tous les types se rapportant au genre. Des synonymies nouvelles sont proposées pour quelques cas particulièrement litigieux. *H. striatula* var. *antillana* Santschi est traité comme une variation individuelle de *striatula* et le nom *antillana* devra donc disparaître de la nomenclature. *H. simplex* Emery comprendra comme variations individuelles, sans nom particulier, les trois espèces ou sous-espèces *satzgeri* Forel, *spurium* Forel et *foreli* Santschi, du Costa Rica, avec une seule localité douteuse du Guatemala. L'espèce décrite comme *Rhopalopone relictæ* Mann est transférée au genre *Holcoponera*, par suite des caractères de transition de *H. mina* sp. nov.-*H. mina*, de la Bolivie et du Pérou, et *H. acuta*, de la Bolivie, sont décrits comme espèces nouvelles.

ACKNOWLEDGMENTS.

I wish to thank Dr. M. R. SMITH for help with the loan of material from the U. S. National Museum and Dr. F. BRYK for a similar loan from the Naturhistoriska Riksmuseet in Stockholm. Dr. J. C. BEQUAERT, Dr. and Mrs. T. EISNER, Dr. ERNST MAYR and Dr. E. O. WILSON have my thanks for their aid in various details of preparation of the manuscript.

LES FACTEURS QUI GOUVERNENT LA PONTE CHEZ LA REINE DES ABEILLES

par

Rémy CHAUVIN

(Station de Recherches Apicoles, Bures-sur-Yvette.)

Une des variables essentielles dans le développement de la colonie d'abeilles est constituée chez l'abeille, comme chez tous les Insectes sociaux, par la ponte de la reine. J'ai montré dans un travail précédent (CHAUVIN, 1950) les inconvénients des mesures de la ponte telles qu'on les a pratiquées jusqu'ici : elles présentent toutes en effet le défaut d'être *a posteriori*. On se borne, en général, à mesurer une certaine surface de couvain à un stade déterminé, et à en déduire combien d'œufs ont été pondus *tant de jours auparavant*. Ceci postule : 1° que la durée du développement des larves est tout à fait fixe ; 2° que le rendement des transformations œufs-larves et larves-nymphes atteint 100 %. Or, la durée du développement larvaire n'est pas si régulière que l'ont cru les anciens auteurs ; elle dépend en effet de la régulation thermique, et celle-ci est sujette elle-même à de grosses variations à la périphérie ; et même, au milieu du nid à couvain, elle ne se réalise pleinement, comme l'a montré BÜDEL (1955), qu'aux plus jeunes stades de l'évolution. Or, non seulement le développement des larves se trouve sous la dépendance de la température, comme chez la plupart des insectes ; mais encore la relation qui unit température et développement varie suivant la race (SOOSE, 1954) : la durée totale de l'évolution passerait ainsi de 10 à 33 jours pour deux abeilles de race différente et à la même température ; et les expérimentateurs ne peuvent contrôler qu'imparfaitement la pureté de la souche avec laquelle ils travaillent. J'ai montré enfin (1950) que, si le rendement de la transformation œufs-larves atteint 90 %, celui de la transformation larves-nymphes peut varier de 80 à 72 % ; et nous ne connaissons guère les facteurs qui régissent cette variation ; par conséquent toute méthode indirecte doit être proscrite, et il faut, pour étudier congrûment la ponte, s'attacher au dénombrement des œufs eux-mêmes ; ce qui offre d'ailleurs l'avantage d'une bien plus grande rapidité.

Techniques. J'ai décrit ailleurs (1950) la technique utilisée pour le comptage des œufs et je n'y reviendrai pas. Elle consiste schématiquement à coller sur une plaque de verre une feuille de cire gaufrée et à la placer dans une forte ruche dont les ouvrières étirent la cire en cellules. Ces cellules n'ont pas de fond propre : il est constitué par la plaque de verre.

Il est alors très facile de constituer avec le demi-rayon ainsi disposé un nucléus où l'on introduit une reine féconde et quelques milliers d'abeilles. La ponte commence normalement et on peut la suivre très facilement par transparence, sans toucher à la ruchette. Il faut toutefois tenir compte du fait qu'un certain nombre d'œufs éclosent et sont comptés comme larves jeunes ; d'autres œufs peuvent être pondus dans le même temps ; si bien qu'à moins de repérer exactement chaque cellule ce qui est pratiquement impossible, un nombre d'œufs trouvé sans changement pendant deux jours de suite peut correspondre en réalité à une nouvelle ponte. Les résultats bruts ne peuvent donc être acceptés tels quels ; mais il faut les corriger à l'aide d'une formule mathématique simple (CHAUVIN, 1950).

Résultats. Les comptages ont été poursuivis en 1950 sur un seul nucléus de grande taille, à très forte population, et de grandes dimensions ; en 1953 sur 5 nucléi, et en 1955 sur 7 ; mais je ne mentionnerai ici que ceux qui ont franchi toute la saison sans accident. Les œufs étaient comptés journellement ou tous les deux jours.

Dès 1950, j'avais noté que la ponte n'était nullement régulière, mais se composait d'une *série de cycles* imprévisibles, très irrégulièrement espacés. Cette impression d'extrême variabilité n'a fait que se renforcer à l'examen des résultats de 1953 et 1955. Même avec des reines sœurs, introduites en même temps dans les colonies, avec les mêmes quantités d'abeilles, les cycles ne coïncident nullement. Ce fait suffirait à exclure l'intervention d'une cause extérieure, puisqu'il n'existe peut être pas deux nucléi qui se comportent de la même façon ; ou, tout au moins, les facteurs de variabilité attribuables à des causes internes sont si considérables qu'ils surclassent de beaucoup les facteurs externes.

Un facteur interne qui paraîtrait gouverner le phénomène, à un observateur superficiel, serait *l'encombrement du nid à couvain*. Il va de soi que, lorsqu'une bonne reine a garni complètement toute la surface du rayon, sa ponte s'arrête, puisqu'il ne lui reste plus de cellules où introduire son abdomen. Mais, en fin de saison, lorsque la ponte se ralentit, de très larges espaces restent libres autour de la zone centrale à laquelle la reine restreint progressivement sa ponte ; elle ne cherche pourtant nullement à y aller pondre, alors qu'en pleine saison les œufs sont vraiment logés dans toutes les zones disponibles.

On pourrait déduire de tout cela que l'organisme homéotherme formé par la colonie en arrive à ne plus dépendre que de son mécanisme interne, quel que soit ce mécanisme ; non seulement en ce qui concerne la température, mais aussi pour la fécondité de la reine. Il existe cependant des *facteurs limitant la fécondité* ; j'en ai sommairement étudié deux, tenant à l'apport glucidique et à l'apport azoté et vitaminique.

Influence d'un apport glucidique. Ces nucléi, dont la surface est égale à la moitié de celle d'un cadre Dadant et qui ne peuvent par conséquent admettre qu'une population relativement réduite doivent être nourris constamment au sirop de sucre, et ne peuvent subvenir à leurs besoins. Or l'interruption du nourrissage pendant un temps assez bref de l'ordre de

trois jours stoppe à peu près complètement la ponte, qui reprend dès la redistribution de sirop. Il s'agit d'ailleurs d'un phénomène banal, bien connu des apiculteurs : dans la ruche en état de carence alimentaire, la ponte de la reine s'arrête dès le début.

Les apports azotés. Plus intéressants sont les effets des apports de matériaux azotés : je les ai constitués de pollen ou de gelée royale mélangés au miel dans la proportion de 10-15 p. 100, et administrés journellement à la dose d'une cuillère à soupe de miel par vingt-quatre heures. On notera sur la courbe la remontée rapide de la ponte après une telle alimentation.

Par exemple, du 5 août au 1^{er} septembre 1953, au moment de l'effondrement annuel de l'élevage, des ruchettes A. B. C. ont donné par jour :

A (gelée royale	73 œufs par jour ;
B (pollen)	79 œufs par jour ;
C (témoin au miel seul) ;	31 œufs par jour.

En 1955, du 10 au 31 août :

D (pollen)	98 œufs par jour ;
E (témoin)	47 œufs par jour.

Quelles peuvent être les causes d'une différence aussi considérable dans les pontes ? J'ai évoqué tout à l'heure l'*apport en azote*. Il est évident qu'il n'est probablement pas seul en cause, puisque GONTARSKI a montré qu'une substance extraite du pollen pouvait exercer la plus grande influence sur le développement des organes internes de l'abeille ; PAIN a prouvé aussi l'influence des vitamines du groupe B sur le développement des ovaires, et ses recherches sont corroborées par celles de SCHWARZ et KOCH (1955), bien que MAURIZIO (1954) tende à croire que seul l'azote et non les vitamines importent pour la croissance ovarienne. Cependant des essais poursuivis avec une *Torula* utilisée comme substitut du pollen ont montré une accélération de ponte comparable à celle obtenue avec le pollen. Mais il faut reconnaître que ces levures possèdent, comme le pollen une foule de facteurs accessoires sans doute importants au point de vue vitaminique. Tant que la caséine pure exempte de vitamines, ou toute autre substance protéique purifiée, n'aura pas été essayée, il sera impossible d'affirmer que l'apport d'azote est seul en cause dans l'augmentation de la ponte de la reine.

A vrai dire, on connaît depuis longtemps les bons effets d'un supplément azoté dans l'alimentation des abeilles (voir par exemple HAYDAK et TANQUARY, 1943), mais les tests adoptés pour juger de l'efficacité de telle ou tel produit, comparé au pollen comme étalon, ont toujours été *relatifs aux ouvrières* : pourcentage de mortalité, poids et teneur en azote de l'organisme, quantité de larves amenées à la nymphose ; on ne s'était pas préoccupé de rechercher l'effet de tels produits sur la ponte de la reine.

Après alimentation au pollen ou aux levures, les ouvrières dégagent sur les larves du premier âge, avec la bouillie royale, des traces de pigment

brun, provenant sans doute des substances ingurgitées. Notons aussi que l'adjonction de pollen en quantités massives au miel de nourrissage ne semble ni favoriser ni inhiber la récolte du pollen par les butineuses.

L'arrêt automnal. Lorsque arrive le mois de septembre, la ponte s'effondre, et aucun nourrissage azoté ou sucré n'y fait rien. A vrai dire, on assiste

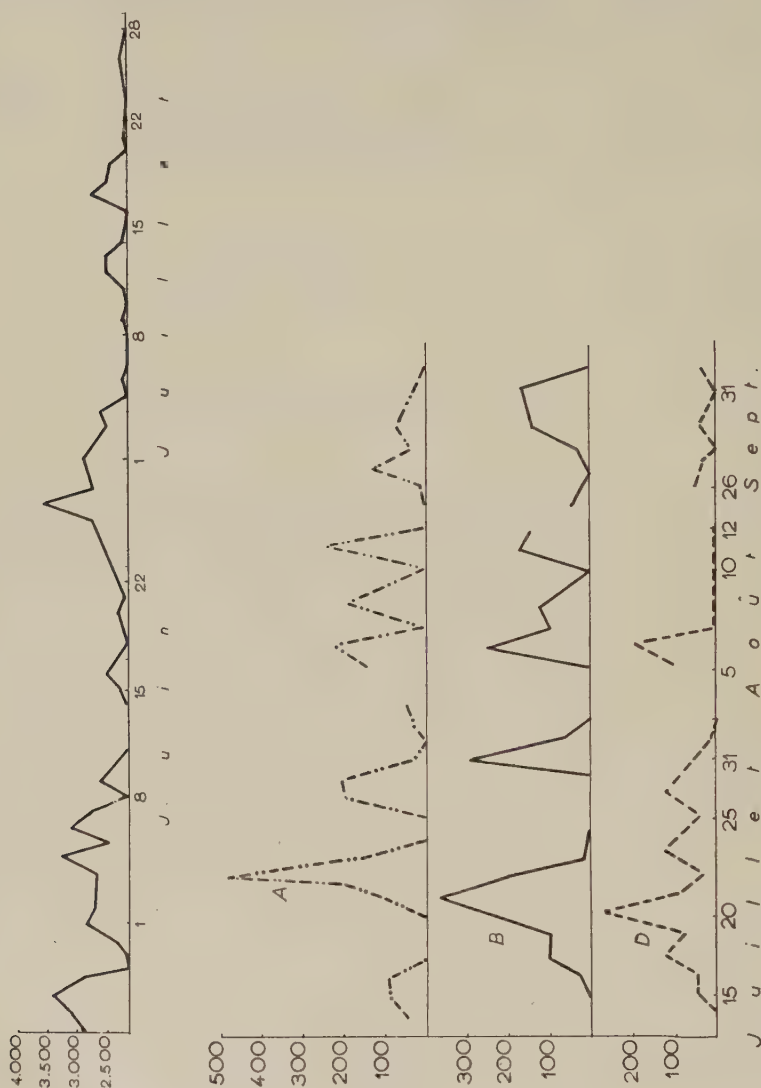


Fig. 1.

Fig. 1. 2. — Cycles de ponte de la reine dans les nœuds unifaces. Fig. 1 : La figure supérieure correspond à un seul nœud de grande taille ; année 1950. En dessous, ABD, trois nœuds étudiés en 1953. Fig. 2 : BIDH, quatre autres observés en 1955. En P, distribution de pollen, les autres nœuds ne recevant que du miel ; notez, surtout en B, la montée brutale de la courbe de ponte. En ordonnées nombre d'œufs.

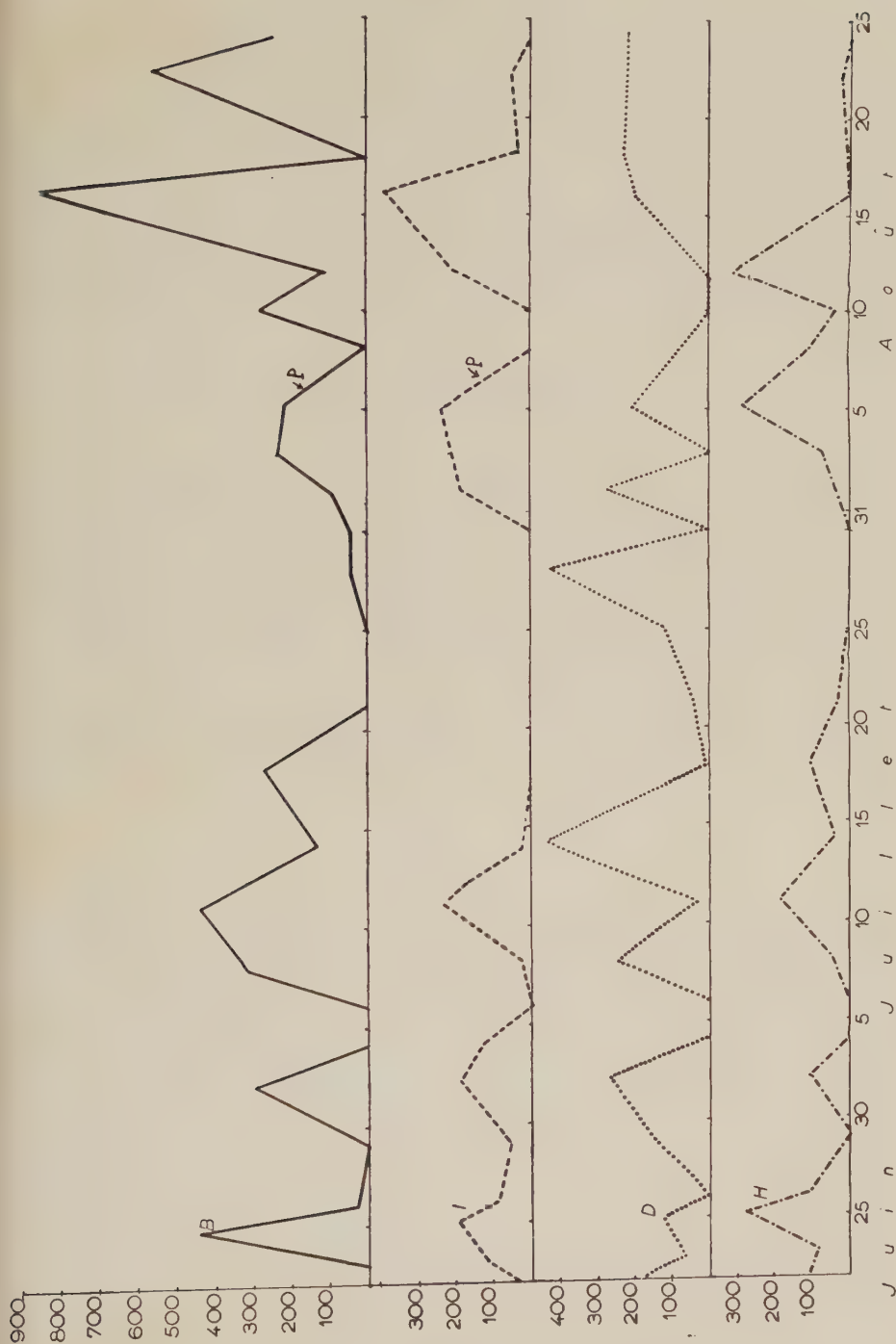


Fig. 2.

très souvent à la ponte de quelques œufs (une dizaine par nucléus et par mois) jusqu'en novembre ou décembre, et la ponte montre aussi un démarrage (dans le Bassin Parisien) vers la mi-février. Mais les causes de l'arrêt automnal ne sont pas élucidées pour cela. En effet, la carence alimentaire ne peut être en cause, puisque l'azote et le sucre sont administrés journellement en quantités relativement considérables. D'autre part, les nucléi étaient placés à l'intérieur du laboratoire et ne communiquaient avec l'extérieur que par un tube de verre d'une quinzaine de centimètres : il semble donc qu'on doive exclure aussi une influence possible du refroidissement extérieur. A moins que la *durée du jour* ne soit en cause (et l'on n'ignore pas l'influence des radiations et de la durée du nyctémère sur le développement voir par exemple travaux de DICKSON), je me demande s'il ne s'agit pas d'une *véritable diapause* ; mais elle ne se manifesterait en tout cas que dans les races d'abeilles de nos régions, car le rythme annuel de ponte des reines est bien différent dans le midi.

RÉSUMÉ. — L'observation journalière de la ponte de la reine des abeilles permet de mettre en évidence la grande indépendance de ce phénomène par rapport aux conditions extérieures. Seule la carence alimentaire poussée assez loin paraît capable d'arrêter la ponte. Dans ce cas, l'apport de matériaux purement glucidiques provoque un nouveau départ. Mais, si on ajoute au sucre du pollen et de la gelée royale qui fournissent de l'azote et sans doute aussi d'autres substances annexes (peut-être de nature vitaminique), l'augmentation de la ponte atteint le double de celle des témoins. Il existe enfin un *arrêt spontané automnal* que même le renforcement de l'alimentation ne peut briser, et qui semble pouvoir être attribué à une diapause.

BIBLIOGRAPHIE.

1955. BÜDEL (A.). — Schwankungen der Lufttemperatur in der Wabengasse eines brütenden Bienuenvolkes (*Z. Bienenforsch.*, **3**, 88-92).
1950. CHAUVIN (R.). — Méthodes d'observation continue de la ponte de la reine chez les Abeilles (*"L'Apiculteur"*, *Sect. Scient.*, novembre 1950).
1949. DICKSON (R. C.). — Factors governing the induction of diapause in the oriental fruit moth (*Ann. Entom. Soc. Amer.*, **4**, 511-37).
1943. HAYDAK (M. H.), TANQUARY (M. C.). — Pollen and pollen substitutes in the nutrition of the Honeybee. (*Univ. Minnesota, Tech. Bull.*, **160**).
1954. MAURIZIO (A.). — Pollenernährung und Lebensvorgänge bei der Honigbiene. *Apis mellifica* (*Landwirts. Jahrb.*, *Schweiz*, **68**, 115-82).
1951. PAIN (J.). — Vitamines et développement ovarien chez l'ouvrière d'abeille (*C. R. Soc. Biol.*, **145**, 1505).
1954. SCHWARTZ (I.), KOCH (A.). — Vergleichende Analyse der wichtigsten Wachstumsvitamine der Blütenpollen, nebst einer Bemerkung über die Verteilung der Vitamine im Buchensämlingen (*Wiss. Z. Martin Luther Univ.*, **4**, 1).
1954. SOOSE (E.). — Einfluss der Temperatur auf die Augestaltung von Flügelindex und Panzerfarbe der Honigbiene (*Arch. Bienenk.*, **31**, 49-66).

OBSERVATIONS ON THE GASTRAL DIGESTIVE TRACT IN THE MALE CARPENTER ANT, *CAMPONOTUS PENN- SYLVANICUS* DEGEER (FORMICIDAE, HYMENOPTERA).

by

JAMES FORBES

(*Biological Laboratory, Fordham University, New York 58, N. Y.*)

This paper presents observations on the male gastral digestive organs of *Camponotus pennsylvanicus* DEGEER and reports the structure of the gastral digestive tract prior to the nuptial flight as well as at the swarming for the nuptial flight. These observations indicate that there are differences in the male ventriculus of *C. pennsylvanicus* and of the parasitic ant, *Anergates atratulus*, as recently reported by MEYER (1955).

The material for this study consists of males collected from nests in tree stumps during the month of May and also of males swarming for the nuptial flight from a nest on a late afternoon in July. The observations now reported were made at the time of previous studies. The methods employed in fixing and staining have already been described (FORBES, 1938 and 1954).

The author wishes to extend his sincere appreciation to Doctor E. R. WITKUS, a colleague, for assisting with the photomicrographs in this paper.

MALES FROM NESTS

The organs of the digestive system found in the gaster consist of the crop, the proventriculus or gizzard, the ventriculus or midgut, the intestine with the attached Malpighian tubules, the rectum, and the anus (fig. 1). The crop, a thin-walled sac, is the continuation of the oesophagus as it emerges from the petiole into the gaster. It occupies the anterior part of the first segment and is normally dilated although its size varies with the amount of food it contains. The proventriculus or the complicated gizzard usually extends obliquely downward from the crop to open on the anterior ventral side of the ventriculus. The ventriculus is a large, ellipsoidally-shaped, thick-walled sac extending from approximately the posterior half of the first segment to about the middle of the third gastral segment. The short intestine, a narrow tube, arises from the posterior end of the ventriculus and then bends dorsally to enter the dilated, thin-walled rectum. The Malpighian tubules open separately into the anterior end of the intestine just behind its junction with the ventriculus. The majority of males dissected had 18 tubules, a few had 20, and one had 23; in this latter case, one tubule branched a short distance from its base.

Six rectal pads are on the wall of the rectum, which tapers posteriorly to end at the anus. The anus opens on the eighth gastral segment dorsal to the genitalia (FORBES, 1952). The digestive organs occupy a large part of the gastral cavity. They are surrounded by a moderate amount of fat tissue, which physically serves as a packing tissue to support these gastral organs.

The histology of the organs of this portion of the digestive tract is the

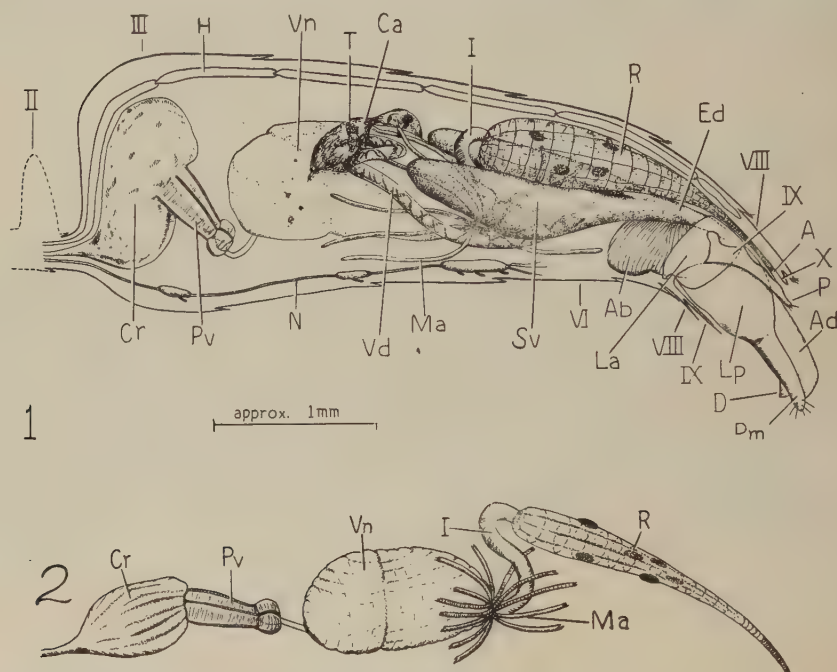


Fig. 1. — Diagram of a lateral dissection of the gaster of the *Camponotus pennsylvanicus* DeGeer male collected from the nest to show the internal organs in position. The left side of the IXth and the Xth terga and the left lateral genitalic valves are still in position. Roman numerals on the dorsal side indicate the abdominal terga and those on the ventral side the abdominal sterna. (From the original of fig. 1, Pl. 1, J. Forbes, *J. Morph.*, 95, 549.)

Fig. 2. — Diagram of the gastral digestive organs of *C. pennsylvanicus* male swarming for the nuptial flight to show the general position and the collapsed condition of the organs; only the attached portion of some of the Malpighian tubules is included. Diagram drawn from sections and to approximately the same magnification as fig. 1.

Abbreviations: A, anus; Ab, aedeagal bladder; Ad, aedeagus; Ca, capsule of testis; Cr, crop; D, digitus volsellaris; Ed, ejaculatory duct; H, heart; I, intestine; La, lamina annularis; Lp, lamina parameralis; Ma, Malpighian tubule; N, nerve cord; P, pygostyle; Pm, paramere; Pv, proventriculus or gizzard; R, rectum; Sv, seminal vesicle; T, testis; Vd, vasdeferens; Vn, ventriculus.

same as has been reported for *C. pennsylvanicus* and *C. americanus* workers (FORBES, 1938 and EISNER and WILSON, 1952) except that there are differences in the epithelium of the ventriculus. In both the male and the worker, the epithelium consists of large secretory cells and replacing

cells built on a basement membrane (figs. 3 and 4). The cytoplasm of the secretory cells is granular and highly vacuolate. It often contains quantities of small basophilic-staining granules; these granules are also present in the ventriculus of *C. americanus* (EISNER and WILSON, 1952).

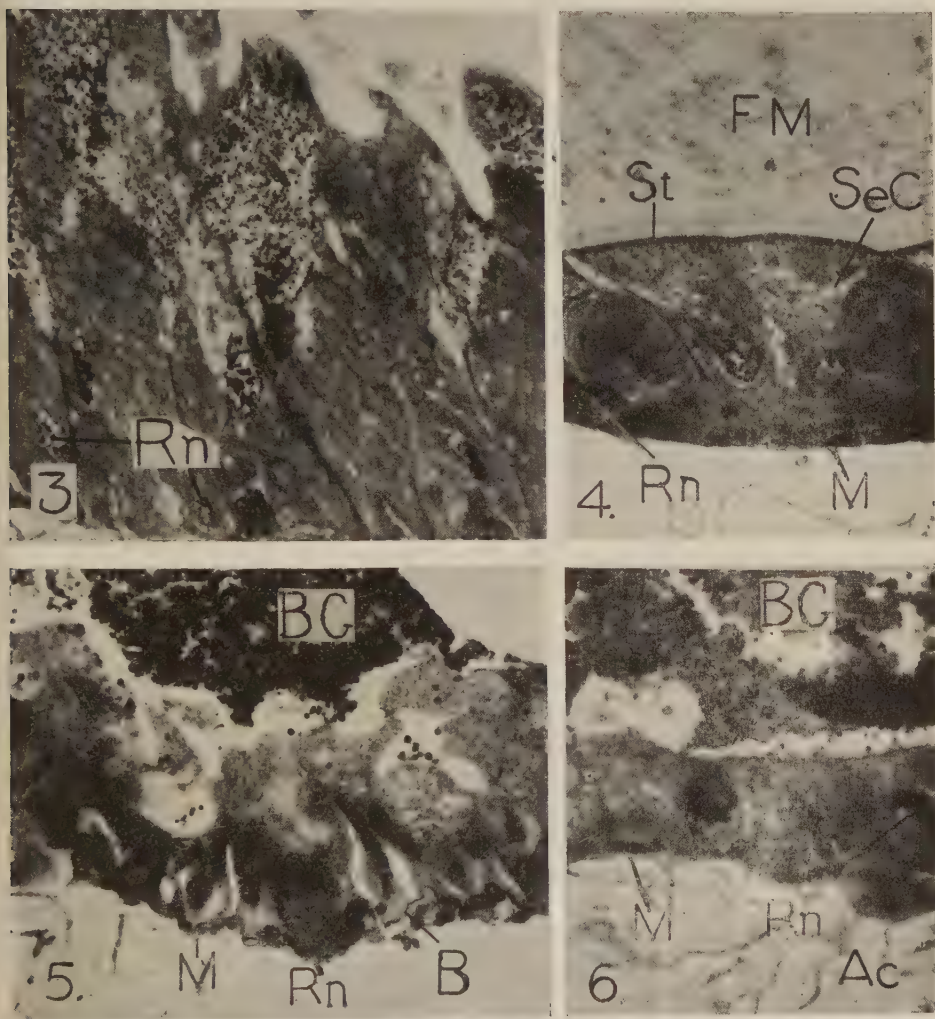


Fig. 3-6. — Photomicrographs of vertical sections through the ventriculus wall of *C. pennsylvanicus* males, X370. 3 and 4 show the normally functioning epithelium of males collected from the nests. 5 and 6 show the disintegrating epithelium of males swarming for the nuptial flight. Note the granules in the cytoplasm of the disintegrating cells. 3 shows the taller cells with their blunt processes, cytoplasm of the secretory cells filled with fine granules, and cytoplasm of replacing cells with many small vacuoles. 4 shows lower cells from the dorsal wall; these cells are similar in height and structure to the cells lining the *C. pennsylvanicus* worker ventriculus. 5 shows disintegrating taller cells. 6 shows disintegrating lower cells.

Abbreviations: Ac, fat cells; B, basement membrane; BC, mass of basophilic granules in lumen; FM, food material in lumen; M, muscle fibers; Rn, replacing cell nucleus; SeC, secretory cell; St, striated border.

The large, vesicular nucleus is filled with prominent chromatin granules. The free surface of these secretory cells tends to be arched or domed and has a distinct striated border. The replacing cells are of different sizes, and they are situated between the secretory cells. Their rather homogeneous and compact cytoplasm is slightly basophilic in staining reaction and has a varying number of small vacuoles present. The granular nuclei of these cells are smaller and more compact than those of the secretory cells. The epithelial cells of the ventriculus are the largest of those of any region of the digestive tract, and the thickness of the wall of this organ is due, almost entirely, to the height of the epithelium. The poorly developed muscle coat consists of scattered, fine, single fibers outside the basement membrane, which course in different directions and which are not organized into distinct layers.

In the worker, the secretory cells of the ventriculus are quite uniform in height. The ventriculus has a large lumen, which contains finely granular, slightly acidophilic-staining food material. In the male, on the other hand, most of the cells are much taller than the worker cells although there are regions on the dorsal wall of the ventriculus where the cells are similar in height and shape to those of the worker (fig. 4). The free surfaces of the secretory cells and of the largest of the replacing cells are extended into blunt processes (fig. 3). The lumen of the male ventriculus, as compared with that of the worker, is much reduced. Food material is also present in the male ventriculus.

SWARMING MALES

The males which were issuing from the nest and swarming for the nuptial flight have their gastral digestive organs collapsed, reduced in diameter, and empty of any food material (fig. 2). The crop is smaller, its walls have collapsed. The epithelial folds, described for the worker (FORBES, 1938), are found in the male crop and here are appressed. The sepals of the calyx portion of the proventriculus are closed. The ventriculus is about one-half its former size, and it shows marked histological changes from its previous condition. On the outside of the ventriculus, the scattered muscle fibers have contracted and are impressed into the basal portions of the epithelial cells; this gives the outer surface a wrinkled, irregular appearance. The secretory and replacing cells are breaking down, and their cytoplasm has vacuoles and spaces with basophilic granules (figs. 5 and 6). The nuclei of the secretory cells are difficult to find and seem to have disintegrated, while those of the replacing cells are irregular in shape and pycnotic. The lumen of the ventriculus is practically filled with a mass of intensely basophilic-staining granules of varying sizes, apparently derived from the disintegrating epithelium. The intestine and Malpighian tubules are the only two organs which show

no changes at swarming. The rectum is collapsed and reduced considerably in its diameter.

The crop, proventriculus, and ventriculus are still surrounded with fat tissue, but they are lying practically on the floor of the first three gastral segments; the crop and proventriculus in the first two segments and the ventriculus in the second and third. Thus, there are large, empty spaces at the anterior end of the gaster. Since at the time of the nuptial flight the bulky organs of the gastral digestive tract collapse and the ventriculus shrinks, it might be possible that these empty spaces are filled with expansions of the tracheal system or tracheal air sacs, which serve to increase the buoyancy of the male.

Anergates atratulus. MEYER (1955) states that the *atratulus* male does not develop a functional, imaginal midgut, and that, in the course of its short life-span, it probably takes no food and dies after many matings when its sperm supply is exhausted. In support of this, he reports that the ventriculus epithelium consists of rather shallow or flattened cells without any replacing cells. Frequently, this epithelium lacks every sign of a secretion, but often one-half of the epithelium shows a holocrine secretion with the remaining half completely functionless. The epithelium becomes completely destroyed in many cases when a single holocrine secretion wave surges through the midgut.

Summary

The anatomy and histology of the digestive organs in the gaster of *Camponotus pennsylvanicus* males are described for those taken from nests during the month of May and for those captured when they were swarming for the nuptial flight in July.

The arrangement of the organs and their histology are similar to that which has already been described for the *Camponotus* workers. In the male ventriculus, however, the epithelial cells are taller and their shapes somewhat different from those in the worker. There is food in all the male gastral digestive organs.

Most males dissected had 18 Malpighian tubules, some had 20, and one had 23; in this latter case, one was branched.

In the swarming males most of the gastral digestive organs are collapsed or reduced in diameter. The crop, proventriculus, and ventriculus are practically lying on the floor of the first three gastral segments; this condition leaves large spaces in the dorsal anterior end of the gaster. The system is empty of food. The epithelial cells of the ventriculus are degenerating, and the lumen of this organ is filled with basophilic-staining granules.

There are differences between the midguts of *C. pennsylvanicus*, here described, and of *Anergates atratulus*, described by MEYER (1955).

Résumé.

Description anatomique et histologique des organes du tube digestif de *Camponotus pennsylvanicus* mâles pris dans leurs nids durant le mois de mai ou saisis pendant l'essaimage nuptial en juillet.

La position des organes et leur histologie sont semblables à celles qui ont été déjà décrites pour les *Camponotus* ouvrières. Dans le ventriculus du mâle, pourtant, les cellules épithéliales sont plus longues et leur forme est quelque peu différente de celles de l'ouvrière. Tous les organes digestifs gastriques du mâle contiennent de la nourriture.

La plupart des mâles disséqués avaient 18 tubes de Malpighi; d'autres en avaient 20, un en avait 23; dans ce dernier, il y avait des tubulibranches.

Chez les mâles essaimants, la plupart des organes digestifs gastriques sont affaîssés ou réduits en diamètre. Le jabot, le gésier et le ventriculus reposent pratiquement sur le fond des trois premiers segments gastriques; cette position libère de grands espaces dans la partie antéro-dorsale de l'abdomen. Le système digestif est vide de nourriture. Les cellules épithéliales du ventriculus sont en dégénérescence et la cavité de cet organe est remplie de grains intensément colorables par l'hématoxyline.

Il y a des différences entre le ventriculus de *C. pennsylvanicus*, décrit ici, et celui de *Anergates atratulus*, décrit par MEYER (1955).

Zusammenfassung.

Die Anatomie und Histologie der Verdauungsorgane im Gaster des männlichen *Camponotus pennsylvanicus* werden beschrieben auf Grund von Exemplaren, die im Mai aus dem Nest genommen und im Juli während der Hochzeitsflug gefangen wurden.

Die Verteilung der Organe und ihre Histologie sind ähnlich denen der Arbeiter von *Camponotus*, die schon früher beschrieben wurden. Im männlichen Mitteldarm sind allerdings die Epithelzellen höher und ihre Form ist etwas anders als im Mitteldarm des Arbeiters. Nahrung ist vorhanden in allen männlichen Verdauungsorganen des Gasters.

Die meisten untersuchten Männchen hatten 18 Malpighische Gefäße, einige hatten 20 und eines hatte 23; in letzterem Falle war einer der Gefäße verzweigt.

In den Männchen in Hochzeitsflug sind die meisten Verdauungsorgane des Gasters zusammengefallen, oder ihr Durchmesser ist reduziert. Der Kropf, der Vormagen und der Mitteldarm liegen praktisch am Boden der drei ersten gastraln Segmente. Dieser Zustand läßt große Räume in der dorsalen Vorderende des Gasters frei. Das System enthält keine Nahrung. Die Epithelzellen des Mitteldarms degenerieren und das Lumen dieses Organs ist voll mit basophilen Körnchen.

Es bestehen Unterschiede zwischen dem hier beschriebenen Mitteldarm

von *C. pennsylvanicus* und dem von *Anergates atratulus*, welcher von MEYER (1955) beschrieben wurde.

LITERATURE CITED

1952. EISNER (T.), WILSON (E. O.). — The morphology of the proventriculus of a formicine ant (*Psyche*, **59**, 47-60).
1938. FORBES (J.). — Anatomy and histology of the worker of *Camponotus herculeanus pennsylvanicus* De Geer (Formicidæ, Hymenoptera) [*Ann. Ent. Soc. Amer.*, **31**, 181-195]. — 1952. The genitalia and terminal segments of the male carpenter ant, *Camponotus pennsylvanicus* DeGeer (Formicidæ, Hymenoptera) [*Jour. N. Y. Ent. Soc.*, **60**, 157-171]. — 1954. The anatomy and histology of the male reproductive system of *Camponotus pennsylvanicus* DeGeer (Formicidæ, Hymenoptera) [*J. Morph.*, **95**, 523-555].
1955. MEYER (G. F.). — Untersuchungen an einer parasitischen Ameisen (*Anergates atratulus* Schenck) [*Insectes Sociaux*, **2**, 163-171].
-

BEOBSACHTUNGEN UEBER DIE GYNANDROMORPHEN HONIGBIENEN, MIT BESONDERER BERUECKSICHTIGUNG IHRER HANDLUNGEN INNERHALB DES VOLKES (1)

von

SHOICHI F. SAKAGAMI und HIROYA TAKAHASHI (2)

(Zoologisches Institut d. Naturwiss. Fakultät an der Hokkaido Universität).

Seit dem bekanntesten Beispiel des Eugster-Stockes erschienen die gynandromorphen Honigbienen wiederholt unter verschiedenen Umständen. Heute haben wir darüber genaue morphologische Untersuchungen, sowie Hypothesen bezüglich ihrer Entstehung (s. MEHLING '15). Neuerdings wurde auch ihre genetische Analyse in Angriff genommen (ROTHENBUHLER *et al.* '52). Trotzdem wissen wir darüber noch so gut wie gar nichts, wie diese abnormen Individuen sich am Volksleben beteiligen und in welcher Weise sie von ihren normalen Volksgenossen behandelt werden.

Wir konnten im Sommer 1953 die Gelegenheit ergreifen, an einer ziemlichen Menge Gynandromorpher einige Beobachtungen zu machen. Alle diese Individuen stammten aus einer Königin von der unreinen italienischen Rasse (*Apis mellifera ligustica*) wie die meisten Bienenstöcke japanischer Imker. Sie wurde in Juli von einer ihrer Töchter entthront (UCHIDA u. SAKAGAMI '55, Volk B'). Da aber die letztere wieder manche Gynandromorphe produziert hat, wurden insgesamt ungefähr 40 Individuen aus diesem Volk gewonnen.

MORPHOLOGIE DER AEUSSEREN CHARAKTERE

Die Beschreibungen der äusseren Merkmale der gynandromorphen Bienen wurden schon von Mehling u. a. so eingehend gegeben, daß wir sie nur kurz erwähnen. Manche Individuen gingen vor der morphologischen Prüfung schon während Beobachtung ihrer Handlungen verloren. Aber alle gefundenen Individuen gehörten zum ergatandromorphischen Typ. Natürlich stimmten sie in ihrer Körpergröße mit der Arbeiterin, nie aber mit der Drohne überein.

(1) Beitrag Nr. 338 aus dem Zool. Institut, Naturwiss. Fakultät, Hokkaido Univ., Sapporo, Japan.

(2) Unter der Anleitung von Herrn Prof. Tohru Uchida wurden die histologische Untersuchung von Takahashi, die anderen Beobachtungen von Sakagami ausgeführt.

Kopf: Außer den Individuen, deren Kopf äußerlich vollkommen eingeschlechtlich war, wurden verschiedene Uebergangsformen von ♂♂-Kombinationen wie folgt gefunden.

Fazettenaugen: Verschiedene Uebergangsformen (s. Abb. 1).

Stirnaugen: In ihrer Stellung meistens lateralasymmetrisch. Nämlich es liegen



Abb. 1. — Verschiedene Typen der gefundenen Gynandromorphen. Bei einigen Individuen sind auch die Keimdrüsen und der Stachel abgebildet. Zur Individuumsbezeichnung siehe Fussnote (1).

zwei schief nebeneinander entlang dem inneren Fazettenaugenrande (männlich), die dritte liegt demgegenüber auf dem gegenseitigen weiblichen Scheitel.

Fühler: Bei je 2 und 6 Individuen vollkommen ♀ bzw. ♂.

Bei 13 Individuen dagegen an einer Seite männlich (13-gliedrig) und an der anderen weiblich (12-gliedrig). Ferner bei zwei Stücken (Nr. FM-8, FM-9)(1) ein feineres

(1) Individuumsbezeichnung: alle Gynandromorphen wurden der Struktur ihres Kopfes gemäß in fünf Gruppen eingeteilt und darin je eine numerische Bezeichnung gegeben (F und M: mit vollkommen ♀ bzw. ♂ Kopf, FM: ungefähr vollkommene Lateralasymmetrie, Mf u. Fm: ungleiche Lateralasymmetrie mit stärkerem Ueberwiegen eines Geschlechtes).

Mosaik (Stiel ♂, die sonstigen Teile ♀). *Oberkiefer*: Bei 5, 13 und 3 Individuen je ♀ ♂♂ und ♂. Zwei Stücke zeigen feineres Mosaik (fM-2 ♂ : ♂♂, fM-4 ♂ : ♀♂). *Kopfschild*: ♀ 7, ♀♂ 2, ♀♂ 13 und ♂ 8 Individuen. fM-1 und fM-4 zeigen feineres Mosaik.

Zunge, Farbe und Behaarung zeigen meistens eine verhältnismäßig deutliche Lateralasymmetrie. Betrachtet man die verschiedenen Merkmalen zusammenfassend, so gehören alle untersuchten Stücke zu je einer der fünf Gruppen mit dem folgenden Verhältnisse : F (4), fM (3), FM (10), fM (11) und M (11). Daraus erkennt man, sofort ein Ueberwiegen der männlichen Elemente im Kopf der untersuchten Individuen.

Brust: Durch die geringe Entwicklung der sekundären Geschlechtsmerkmale an der Brust wird es, bei manchen Individuen, erschwert, deren geschlechtliche Zugehörigkeit klar zu machen. Aber wenigstens kommt bei 7 Individuen irgendwelche Lateralasymmetrie in Bezug auf Behaarung oder Gestalt der Brust vor. Infolge der dichten hellfarbigen Behaarung, hebt sich das helle Aussehen der weiblichen Hälfte oft scharf von der dunklen männlichen Seite ab. Auch wird, bei einigen Individuen, wegen der ungleichen Rechts-Links-Entwicklung eine Verziehung der ganzen Brust beobachtet. Die Längen der beiden Vorderflügel weichen bei 12 Individuen voneinander ab. Mit Ausnahme von FM-2, was später nochmals erwähnt werden wird, wurden keine feineren Mosaik der Beinstruktur wie beobachtet von Mehling, bei den hinsichtlich der Beine lateralasymmetrischen Individuen gefunden.

Hinterleib: Die meisten Individuen besitzen 6 Segmente wie bei normalen Arbeiterinnen. Nur kommt bei drei Individuen, d. h. fM-5, FM-7 und FM-8, ein sehr degeneriertes 7 Segment vor. Teilt man 39 untersuchte Individuen nach ihren Hinterleibsmosaiken ein, die, wie in Abb. 1 teilweise reproduziert wurde, sehr variabel waren, so beträgt das Verhältnis der Indiv.-Zahl in jeder Gruppe wie folgt : ♀ 11, ♀♂ 8, ♂♂ 8, ♂♂ 8 und ♂ 4. Ferner in den äußeren Genitalien, obwohl eine geringere Indiv.-Zahl, ♀ 21, abnorm-♀ 3, abnorm-♂ 3. Es überwiegen nämlich in der Verteilung der sekundären Geschlechtsmerkmale am Hinterleib, im Gegensatz zum Kopf, deutlich die weiblichen Elemente.

HISTOLOGIE DES GEHIRNES UND DER KEIMDRÜSEN

Um den Grad der inneren Mosaik ins klare zu setzen, wurden das Gehirn und die Keimdrüsen einiger Individuen histologisch beobachtet (Bouin, 10 μ Serienschnitt, D.-Hämatoxylin u. Eosin).

Nach JONESCU '09 unterscheiden die Gehirne der Drohne und der Arbeiterin sich durch die Seh- und Riechzentren, doch vor allem durch die Pilzkörper. Die Höhlung der beiden äußeren und inneren Becher des Pilzkörpers ist bei der Arbeiterin größer und tiefer als bei der Drohne. Außerdem erweitern sich bei der Arbeiterin die Vorder- und Hinterwände des Bechers so hervorragend, daß sie beinahe den Protocerebrallobus berühren. Die Riechzentren der Arbeiterin sind größer als die der Drohne. Dagegen sind die Sehzentren der Drohne, entsprechend ihren vergrößerten Augen, bemerkenswert größer als die der Arbeiterin. Infolgedessen werden sie in einer frontalen Schnittserie früher als die der Arbeiterin sichtbar.

Prüft man nach diesen Merkmalen die Serienschnitte unserer gynandromorphen Gehirne, so wird ein ziemliches Entsprechen zwischen dem äußeren und inneren Mosaik festgestellt. Besonders gilt das klar von der fM-Gruppe hinsichtlich einer Lateralasymmetrie der Größe der Seh- und Riechzentren sowie der Größe und Stellung der Becher (Abb. 2, FM-3, u. Abb. 3 b), und, ausgenommen die Größe der Sehzentren, auch von der

fM-Gruppe (Abb. 2, fM-4, Abb. 3 c). Andererseits zeigt das Gehirn von Fm-1 (Abb. 2, Fm-1, Abb. 3 a) die Arbeiterinnencharaktere beinahe vollkommen, folglich keine deutliche Lateralasymmetrie in den Bechern wie bei den obigen Gruppen. Jedoch entwickelt die Hinterwand ihren rechten Becher nicht so gut wie an der linken Seite. Also scheint die Beimischung irgendwelcher männlichen Elemente in diesem Gehirn nicht immer undenkbar. Das Gehirn der M-Gruppe repräsentiert im allgemeinen den beinahe

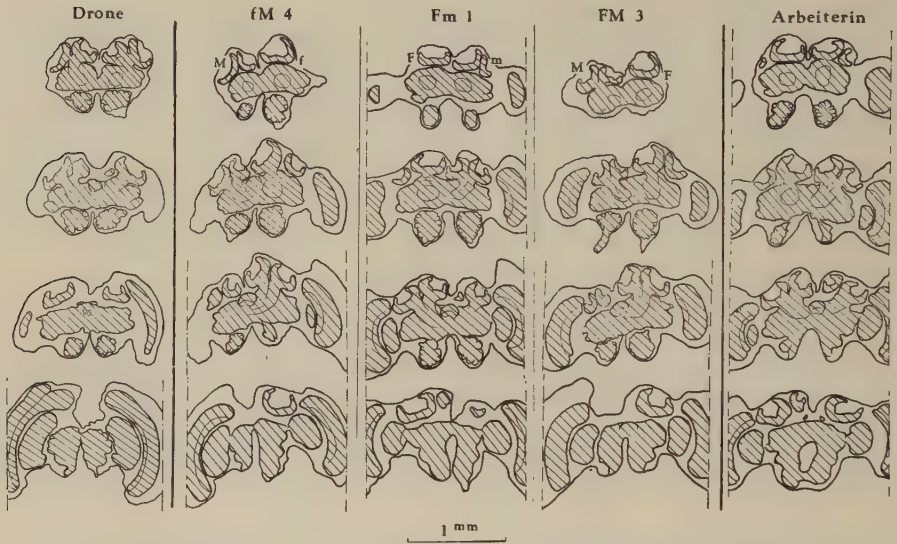


Abb. 2. — Frontalschnitte der Gehirne von Drohne, Arbeiterin und drei Gynandromorphen. Von vorne nach hinten aufeinanderfolgende und nach der Lage entsprechende Schnitte. Fibrillärmasse schraffiert gezeigt.

vollkommenen Drohnentyp. Aber bei einem Individuum (M-5, Abb. 3 e) sieht die Höhlung der Becher tiefer aus als bei der normalen Drohne, und vielmehr dem der Arbeiterin ähnlich. Ferner ist der Hinterrand des linken Bechers von M-6 (Abb. 3 d) so viel mehr entwickelt als der des rechten, daß er bis zu den hinteren Querschnitten verfolgt werden kann. Da solche Erweiterung, wenigstens unseres Wissens, niemals bei normalen Drohnen gefunden wird, ist es wieder nicht undenkbar, daß hierbei eine äußerlich unfeststellbare Beimischung weiblicher Elemente vorkommt.

Die Keimdrüsen verhalten bei 12 anatomisch untersuchten Individuen sich wie folgt: Fm-Gruppe (♂ 1, ♀ 1), FM-Gr. (♀ 2, ♂ 2, ♀♂ 1), fM-Gr. (♀ 2, ♂ 1, ♀♂ 1), M-Gr. (♀ 1, ♂ 1). Die histologische Beobachtung fügt keine neuen Kenntnisse hinzu. Die Entwicklung der Eierzellen in den weiblichen Ovarienteilen ist freilich sehr schwach. Bei FM-5, bei dem auch die Keimdrüsen mosaikartig waren, wurde unter den mit reifen Spermatozoen erfüllten Hoden (Abb. 3 f) eine knochenartige Ovariumstruktur gefunden, worin, wie bei den anderen Individuen, nur die Nährzellen spärlich vorhanden waren (Abb. 3 g).

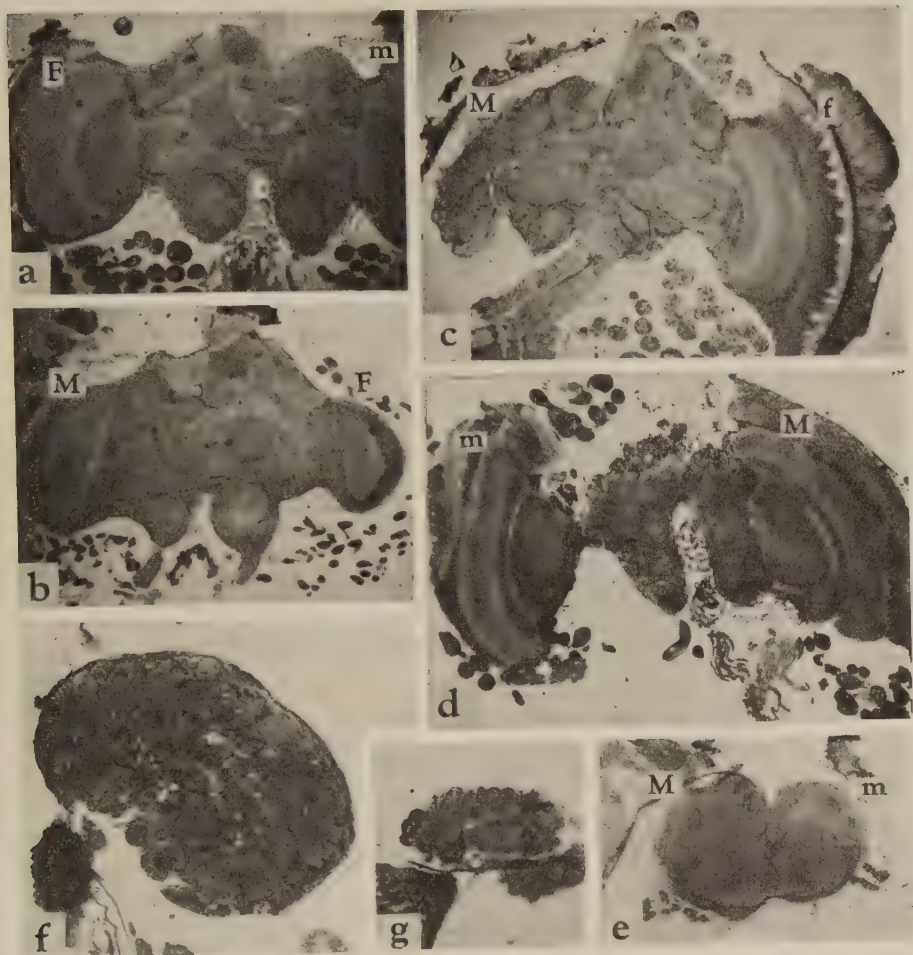


Abb. 3. — Mikrophotographien der Querschnitte durch Gehirn (a-e, $30\times$) und Keimdrüsen (f, g, $50\times$) einigen Gynandromorphen (a, Fm-1; b, FM-3; c, fM-4; d, M-6; e, M-5; f, u, g, FM-5).

HANDLUNGEN INNERHALB DER VOELKCHEN

Ungefähr 20 Individuen von den gefundenen Gynandromorphen, die während Mai bis Juli ausschlüpfen, leiteten wir nach Markierung in zwei Beobachtungsvölkchen ein, die, für einen anderen Zweck, nur aus je 20—30 Arbeiterinnen (ohne Königin) zusammengesetzt worden waren. Andere fünf Individuen, die im Spätsommer gefunden wurden, verpflanzten wir in ein Beob.-Völkchen der japanischen Biene, *Apis indica cerana*, weil wir damals der zweckdienlichen Völker von *Apis mellifera* ermangelten⁽¹⁾.

(1) Ueberpflanzung von *Apis mellifera* Arbeiterin in ein *cerana*-Volk ist nach unserer Erfahrung sehr leicht. Die umgekehrte Operation ist demgegenüber sehr schwer. Darauf möchten wir in Zukunft, zusammen mit verschiedenen biol. Eigentümlichkeiten dieser kleineren Bienenart, eingehend zurückkommen.

Manche Individuen wurden am Tag des Ausschlüpfens, einige andere dagegen erst einigen Tagen nach dem Ausschlüpfen gefunden und eingeleitet. Die letzteren Individuen blieben oft nicht in den ihnen zugewiesenen Volk und verschwanden schon an demselben Tag aus demselben. Wie im Fall von normalen Arbeiterinnen, griffen die älteren Volksgenossen sofort nach Einleitung mehr od. weniger die Gynandromorphen an. Aber der Angriff war im allgemeinen nicht sehr gewaltig, so daß die meisten Gynandromorphen als neue Mitglieder bleiben konnten. Im Fall von *cerana*-Volk, leiteten wir gleichzeitig auch manche Arbeiterinnen von *Apis mellifera* ein. Dabei wurde die Tendenz beobachtet, daß die Arbeiterinnen der japanischen Biene die eingeleiteten Gynandromorphen heftiger angriffen als die normalen *mellifera*-Arbeiterinnen. Beim Angegriffen werden leisteten alle Gynandromorphen keinen Widerstand, sondern antworteten meistens mit der von BUTLER und FREE '52 und von SAKAGAMI '54 beschriebene eigenartige Körperstellung (Unbeweglichkeit, Verbiegung des Hinterleibes, Ausstülpen der Zunge und, sogar bei F-3, Abreißen der ausgestülpten Zunge).

Die Handlungen, die bei Gynandromorphen verhältnismäßig häufig beobachtet wurden, sind als Indiv.-Rekorde in Tabelle 1 und, angeordnet gemäß dem Kopftyp, in Tab. 2 dargestellt. Bevor darüber einzeln zu sprechen ist, möchten wir einige Vorbemerkungen hinzufügen.

1. Allgemeine Bemerkung.

Unsere Gynandromorphen waren ausnahmslos ergatandromorph, nämlich ein Mosaik von Arbeiterin und Drohne. Abgesehen von der Eiablage bei der Weisellosgkeit äußert die Bienenarbeiterin keine Geschlechtshandlungen. Auch verhält die Drohne, wenigstens innerhalb des Volkes, sich keineswegs geschlechtlich. Also kommen hierbei nicht in Frage die primären Geschlechtshandlungen, die bei den gewöhnlichen gynandromorphen Tieren am wichtigsten sind. Ueberdies zeigt die Drohne beinahe keine spezifischen Handlungstypen, wenigstens innerhalb des Volkes. Somit soll unsere Aufmerksamkeit darauf konzentriert werden, ob und wie weit die der Arbeiterin typischen Handlungen bei unseren Gynandromorphen offenbart wurden. Tatsächlich hatten wir nur eine einzige Gelegenheit, wobei eine der Drohne typische Handlung beobachtet wurde, nämlich, die Kotentlastung sofort nach dem Gefangenwerden mit Fingern von M-10, eine beinahe vollkommen männlichen Individuum mit geringer Beimischung weiblicher Elemente am Hinterleib.

Es ist jedoch wohl bekannt, daß beim Herumkriechen auf der Wabe die Arbeiterin sich schnell und lebhaft, die Drohne dagegen langsamer und watschelnd bewegt. Diese Differenz im allgemeinen Bewegungstyp wurde, obwohl nicht quantitativ bestimmt, dem Grad der Beimischung von ♀ od. ♂-Elementen gemäß ziemlich klar beobachtet. Die Individuen mit überwiegenden ♂-Elementen wie M-3, M-5 krochen watschelnd. Andererseits, bei den beinahe weiblichen Individuen wich ihre Bewegungen-

M	T. A.	B. D.	FRESSAKTE					ZELLENDZOGENE HANDLUNGEN		SONSTIGE INTERINDIVIDUELLE HANDLUNGEN				SONSTIGE HANDLUNGEN					
			U. GEGENSEIT. FÜTERUNG							W	Q	q	Hof	t	fan	st	fl	Hob	
	G	G'	g	g'	Sg	P	Zp	B											
F-1	1	10+3	4	5	9	1	3	—	12	1	1	—	13	—	1	2	10	1	—
F-2	?	4+4	2	—	1	—	—	—	—	—	—	—	—	1	—	—	—	1	2
F-3	?	5+4	4	—	3	—	1	1	—	—	—	—	—	—	+2	—	—	3	1
F-4	1	8+2	3	2	4	1	—	—	—	—	—	1	—	—	+4	—	—	4	1
Fm-1	? > 5	11+2	9	13	6	2	5	—	15	1	3+1	—	9	—	3	—	11	4	—
Fm-3	1	6+2	3	2	6	4	—	2	29	2	—	—	6	—	—	2	8	2	—
FM-1	2-3	9	—	3	2	3	5	—	1	—	5	—	1	—	—	—	9	1	—
FM-2	1	10	3	9	6	2	2	—	12	—	5	—	1	—	—	—	7	—	—
FM-3	1	10	5	8	1	3	5	—	20	—	7	—	11	—	—	1	7	2	—
FM-4	1-2	10	3	15	1	5	5	1	40	8	1	—	4	—	—	6	3	1	—
FM-5	?	11+1	8	11	13	20	4	1	32	4	1	—	4	—	—	—	3	1	—
FM-6	1	5+1	3	2	1	1	—	—	11	—	—	—	6	—	—	1	3	4	—
FM-10	?	5+3	2	—	3	—	—	—	—	—	—	—	—	1	—	—	—	—	—
fM-1	? > 5	12+1	8	6	7	7	—	—	25	1	0+1	—	9	—	—	—	3	2	—
fM-3	»	13+2	3	14	6	3	1	—	—	—	0+2	—	11	—	1	2	10	2	—
fM-4	»	7+1	7	14	4	3	—	—	4	1	1	—	—	—	—	—	—	—	—
fM-5	1	3	—	2	—	—	—	—	—	3	—	—	1	—	—	—	—	1	—
fM-7	? > 5	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
M-1	?	8	—	14	5	13	—	1	31	—	—	1	6	—	—	—	1	2	—
M-2	?	3	—	—	—	—	—	—	11	—	—	—	3	—	—	2	1	1	—
M-3	1	4	—	—	—	—	—	—	1	—	—	—	4	—	—	—	—	1	—
M-5	1	11	1	26	17	25	5	—	29	—	—	1	14	—	—	—	3	—	—
M-6	1	10	1	7	6	4	2	1	5	2	0+1	1	17	—	2	2	8	1	—
M-8	?	1	2	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—

Erklärung d. Abkürzungen : M, Individuumszeichnung ; T. A., Tagesalter an Einleitung ; B. D., Beobachtungsdauer (beobachtete u. nicht-beobachtete Tage) ; G, Fütterung d. Genossen infolge Angebelltwerdens ; G', Nichtfüttern trotz Angebelltwerden ; g, Anbellen und Gefüttertwerden ; g', Anbellen, aber nicht Gefüttertwerden ; Sg u. P, Selbstaufnahme von Honig u. Pollen ; Zp, Dauerruhe in Zelle ; B, Bauakte ; W, Wachen gegen Ankömmlinge (Wachen gegen Bleistiftbewegung außerhalb des Glasfensters ist mit + hinzugefügt) ; Q u. q, Ausführung und Erleiden d. Schüttelbewegung ; Hof, Betätigung am Hofstaat ; t, Tanzfolge (ein daran anschließendes Ausliegen ist mit + bezeichnet) ; fan, Fächeln innerhalb des Kastens ; st, Sterzen ; fl, Auflug ; Hob, Hobeln.

Erklärung d. Abkürzungen : M, Individuumszeichnung ; T. A., Tagesalter an Einleitung ; B. D., Beobachtungsdauer (beobachtete u. nicht-beobachtete Tage) ; G, Fütterung d. Genossen infolge Angebitteltwerdens ; G', Nichtfüttern trotz Angebitteltwerdens ; g, Anbitteln und Gefütterwerden ; g', Anbitteln, aber nicht Gefütterwerden ; Sg u. P, Selbstaufnahme von Honig u. Pollen ; Zp, Dauerruhe in Zelle ; B, Bauakte ; W, Wachen gegen Ankömmlinge (Wachen gegen Bleistiftbewegung außerhalb des Glasfensters ist mit + hinzugefügt) ; Q u. q, Ausführung und Erleiden d. Schüttelbewegung ; Hof, Beteiligung am Hofstaat ; t, Tanzfolge (ein daran anschließendes Ausfliegen ist mit + bezeichnet) ; fan, Fächeln innerhalb des Kastens ; st, Sterzeln ; fl, Aufzug ; Hob, Hobeln.

weise nicht stark von derjenigen der normalen Arbeiterin ab. Außerdem, verhielt FM-3, die außer dem Kopf vollkommen weiblich war, sich eher lebhafter als die normalen Volksgenossen. Ferner wurden in sämtlichen Beobachtungen keine unkoordinierten Handlungen od. *Mosaik von Handlungen* nachgewiesen. Alle Handlungen der Gynandromorphen zeigten stets eine gute Koordination. Nur eine zweifelhafte Ausnahme wurde bei M-6 beobachtet: dieses Individuum antwortete einmal gegen ein ankommendes Mitglied durch einen ordentlichen Vorstoß mit ausgestreckten Fühlern und Vorderbeinen, doch geschah dieser Stoß in einer falschen Richtung.

2. Selbstfutteraufnahme und Fütterung der Volksgenossen.

Tabelle I lehrt, daß manche Gynandromorphe, unabhängig von Kopftyp, selbst fressen können. Selbsthonigaufnahme wird, natürlich nicht zu häufig, unter Umständen auch bei normalen Drohnen beobachtet (SAKAGAMI '53 a). Jedoch war der Freßakt bei Individuen mit dem lateralasymmetrischen Kopf, besonders bei FM-Gruppe, infolge des abnormen Mundwerkzeuges sehr steif.

TABELLE 2.

Beobachtungsfrequenz geordnet nach den verschiedenen Kopftyp-Gruppen.

GRUPPE	GESAMT- INDIV.- ZAHL		G			g									
	BEOB. DAUER (Tag.) (1)		G	G'	$\frac{100 \cdot G}{G+G'}$	g	g'	$\frac{100 \cdot g}{g+g'}$	W	B	st	fan	Q	Hof	t
F	4	27	13	7	65	17	2	89	1	1	13	2	1+n	1	7
Fm	2	16	12	15	44	12	6	66	4	3	19	2	—	—	—
FM	7	60	24	48	33	27	34	44	19	12	32	8	—	1	—
fM	5	36	18	36	33	17	14	55	4	5	13	2	—	—	2
M	6	42	4	47	8	28	42	40	1	2	13	4	3	1	2

(1) Beobachtete Tageszahl bei jedem Individuum \times Indiv. - Zahl. Andere Bezeichnungen wie in Tabelle 1.

Die normale Drohne füttert niemals andere Volksgenossen. Demnach ist es bemerkenswert, daß bei unseren Gynandromorphen, wie in Tab. 1 und 2 dargestellt, diese Handlung bei allen Kopftypen durchweg, sogar bei M-Gruppe festgestellt wurde. Aus Tab. 2 könnte man vielleicht einen Parallelismus zwischen Abnahme der Fütterung und Zunahme der ♂ Elemente vermuten. Aber die statistische Prüfung zeigt, daß, wenigstens bei dieser Materialgröße, die Differenz nur zwischen Fm- und M-Gruppen innerhalb des Geltungsbereiches liegt. Die Fütterung wurde nicht nur gegen Arbeiterinnen, sondern auch gegen Drohnen, andere Gynandromorphe und, im Völkchen von *cerana*, gegen die Arbeiterinnen von den

beiden Arten verrichtet. Ueberdies, enthalten die Daten des Gefüttertwerdens 8-maliges Nektarabnehmen aus den heimkehrenden Sammlerinnen.

3. Zellenbezogene Tätigkeiten.

Motiviert durch verschiedene Ursachen, besuchen die Bienenarbeiterinnen sehr häufig die Wabenzellen. Freilich nicht so häufig wie bei Arbeiterinnen, wird das unter Umständen auch bei Drohnen beobachtet. Alle unserer Gynandromorphen führten diese Handlungen mit einer von den zusammenlebenden normalen Arbeiterinnen ununterschiedenen Häufigkeit aus.

Nächst dem kommt die Dauerruhe in der Zelle in Betracht, die bei Arbeiterinnen sehr häufig und nicht selten über 1 Stunde hinaus dauernd beobachtet wird (LINDAUER '52). Die Dauerruhe der Drohnen in den gewöhnlichen Wabenzellen gehört nicht zur Sache, da das Hineinkriechen in die Zelle durch ihre Körpergröße unmöglich ist. Andererseits ist ihre Dauerruhe in der größeren Drohnenzelle zwar möglich, kommt jedoch nur selten zustande. Tabelle 1 zeigt die häufige Dauerruhe unserer Gynandromorphen von allen Kopftypen.

Was die Brutpflege anbetrifft, lieferten unsere Individuen uns keine sicheren Daten. Die zwei weiselosen Völkchen produzierten keine Bruten. In einem *cerana*-Völkchen legte die Königin zwar ununterbrochen ab, doch wurde aus einem noch unerklärbaren Grunde nur eine geringe Zahl von Brut aufgezüchtet. Also haben wir über diese wichtige Tätigkeit nur ein einziges und sogar unsicheres Protokoll bei F-4 (VIII 26. gegen eine 2-tätige Brut von *A. i. cerana*⁽¹⁾. Beurteilt nach der dabei beobachteten Körperhaltung und Zeitdauer (1.2'), scheint dies eine tatsächliche Brutpflege gewesen zu sein. Doch können wir das nicht mit Sicherheit behaupten, da ein direkter Fütterungsakt nicht beobachtet wurde⁽²⁾.

In Bezug auf die Bautätigkeit kommen hierbei nur die Feinbauarbeiten in Frage, weil in unseren schwachen Beob.-Völkchen das Aufbauen der Wabe und die darauf bezogenen Tätigkeiten nicht verrichtet wurden. In den Tabellen ist die Ausführung der Feinbauarbeiten durch manche Gynandromorphe gezeigt. Beim Bauakte verarbeiteten diese Individuen meistens nicht ihre eigenen Wachsexsudate, sondern das Baumaterial wurde von anderen Wabenteilen herbeigebracht. Beiläufig möchten wir an dieser Stelle das Verhalten von FM-4 erwähnen :

Während drei Tage (VI 11.-13.) beschäftigte dieses Individuum sich mit Einreiben und Ebnen der Pollenmasse auf das Drahtnetz der Kastenseite. Es verhielt sich dabei ziemlich stereotypisch. Z. B. führte es am VI 11. während der ungefähr 1 Stunde dauernden Beobachtungszeit ausschließlich diese Tätigkeit aus und brachte eine eingeriebene Fläche von ca. 2 cm² Größe zustande. Interessant ist, daß bei diesem Individuum auch die Feinbauarbeit auf der Wabe am häufigsten beobachtet wurde.

(1) Im gemischten Volk züchten die *mellifera*-Arbeiterinnen normalerweise die Bruten von *cerana*.

(2) Bei den meisten Individuen mit mehr od. weniger weiblichen Elementen, sah der Entwicklungszustand der Pharyngealdrüse histologisch wohl funktionell aus.

Ferner haben wir bei M-6 ein Protokoll des Stampfens der Pollenkügelchen, die von einer Pollensammlerin in der Zelle ungestampft übriggeblieben waren.

4. *Kampflustige Handlungen.*

Alle drei Beob.-Völker hatten keine *differenzierte* Wächterinnengruppe. Ob die gynandromorphen Bienen sich am Wächterdienst beteiligen können oder nicht, kann daher unser Protokoll nicht beantworten. Aber die Prüfung der Ankömmlinge mit entgegengestreckten Fühlern und Vorderbeinen und die danach häufig vorkommende momentane Ergreifung wurden bei den meisten Arbeiterinnen und, wie in Tabelle, auch bei den Gynandromorphen von verschiedenen Typen wiederholt beobachtet. Die Reaktion der Gynandromorphen bei Einleitung der neu ausgeschlüpften Arbeiterinnen war verschiedenartig. Z. B. wurde am VI 13. bei der Einleitung einer neuen Jungarbeiterin, infolge des gewaltigen Angriffes durch die älteren Bewohner, ein Bienenball gebildet. Nur zwei Gynandromorphe, fM-4 und FM-3, beteiligten sich nicht an diesem Gedränge. Andererseits griff Fm-1 am VI 16. sehr gewaltig fM-6 an, die an demselben Tag ausgeschlüpft und in das Völkchen überpflanzt worden war. Endlich hielt die erstere den Vorderflügel der letzteren in Munde und zerrte sie aus dem Stock heraus. Ob solche Kampflust irgendwie mit dem Grad des Mosaiks zusammenhängt oder nicht, können wir wegen Materialmangel nicht feststellen.

Interessant ist endlich die Handlung der mit Pinzette aufgepickten Gynandromorphen. Alle Aufgepickten stießen unabhängig vom Körperbau ihren Stachel aus. Sogar bei stark männlichen Individuen wie fM-8, fM-9 u. FM-9 fanden wir beim Aufgepicktwerden an der Spitze des ausgestossenen Stachels einen sezernierten Tropfen von Giftsaft. Tatsächlich verursachte M-6, ein Individuum mit äußerlich vollkommenem ♂-Kopf, dem älteren Verfasser durch Stechen einen Schmerz, der demjenigen durch normale Arbeiterinnen gleich stark war. Auch stieß Fm-3, ein an der Hinterleibsspitze beinahe männliches Individuum, beim Aufgepicktwerden seinen beträchtlich gekrümmten, nicht funktionierenden Stachel aus. Wir müssen jedoch hierbei zwei Leistungen, nämlich, das blosse reflexartige Ausstossen des Stachels und andererseits das Stechen als eine organisierte Handlung besonders betrachten. Die erstere ergibt sich vielleicht ganz automatisch infolge der blossen Krümmung der Hinterleibs, die bei aufgepickten Hymenopteren ohne Rücksicht auf das Geschlecht häufig zustandekommt. Wahrscheinlich beziehen die obigen Beispiele meistens sich auf solchen blossen Reflex, nicht auf das Stechen als eine totale Handlung.

5. *Sonstige interindividuelle Handlungen.*

Die Schüttelbewegung, nämlich eine rasche und kurze dorso-ventrale Körperschwankung auf der Wabe (od. sehr häufig auf dem Körper anderer

Genossen sitzend), geschieht unter Umständen bei manchen Arbeiterinnen nicht selten, obschon ihre Bedeutung uns noch ungeklärt geblieben ist (SAKAGAMI '53 a, MILUM '55). Dabei gibt es oft Arbeiterinnen, die diese Handlung während kurzer Zeitdauer stereotypisch wiederholen. Da auch unseren Völkchen solche Arbeiterinnen vorhanden waren, konnten wir feststellen, daß sie neben Arbeiterin und Drohne gelegentlich auch manche Gynandromorphe als Gegenstand dieses Aktes wählten. Die letztere antwortete, wie bei normalen Arbeiterinnen, auf diese *Alarmierung* (?) mit keinen äußerlich ausgesprochenen Reaktionen.

Auch führten einige Gynandromorphe diese Handlung gegen die anderen Volksgenossen aus. Besonders wiederholte F-3 diese Handlung ganz stereotypisch gegen alle ihr begegnenden Individuen. Bemerkenswert ist, daß diese Handlung auch bei drei M-Typ-Individuen beobachtet wurde, während die normale Drohne keineswegs solcherweise sich verhält.

Die meisten Gynandromorphen wurden in den weisellosen Völkchen beobachtet. Demnach konnten wir die Beteiligung am Hofstaat nur bei drei Individuen feststellen, die in das Völkchen von *A. i. cerana* eingeleitet worden waren. Ihr Benehmen gegen die Königin (von *cerana*) wich wesentlich nicht dem der normalen Arbeiterinnen ab. Ausstrecken der Fühler und Ausweichen vor der ihr entgegenkommenden Königin, od. Betasten der ruhigen Königin mit Fühler, beobachteten wir bei allen drei Individuen (einschließlich M-8!).

Die Gynandromorphen sammelten in den Völkchen weder Nektar noch



Abb. 4. — Individuumsprotokolle über die Handlungen einiger Gynandromorphen. A. Sterzeln von FM-Gruppe (FM-2), B-E. Tanzfolgung durch Gynandromorphe (B. IX 4. 53-11. Tagesalter, C. VI. 15. — 10 + X T. A., D. IX 7. — 7 + X T. A., E. VI 26. — 10 + X T. A.), F. Dauerbeobachtung von F-4 während 22'. Doppellinie: Toilettemachen. Näheres siehe im Texte, G. Pollensammeln durch Fm-2 mit dem mosaikartigen Pollenkörbchen.



Pollen. Der Werbetanz von Gynandromorphen wurde deshalb niemals gefunden. Andererseits, haben wir, wie in Tab. 1 ersichtlich, einige Protokolle darüber, daß sie anderen Tänzerinnen folgten. Jedoch war ihr Interesse für die Tänzerin sehr gering und ihre Folgespur sehr unvollkommen. Die Abb. 4 B-E schildern einige Spuren solcher Tanzfolge.

Meistenfalls hörten sie mit dem Folgen mitten im Kreislaufen auf, bald infolge gelegentlichen Zusammenstossens mit einer herbeikommenden Kameradin, bald infolge der bei lässigem Folgen verursachten Zunahme der Entfernung von der Tänzerin. Ein verhältnismäßig vollkommenes Folgen wurden nur bei F-3 und F-4 gesehen (Abb. 4). Anschließend an solches Folgen krochen diese zwei Gynandromorphen erregt herum und flogen oft ins Freie fort. Aber niemals konnten wir die daraus zufolgernde Sammeltätigkeit feststellen. Immer kehrten sie heim, weder Pollen noch Nektar tragend, kein erregtes Herumkriechen auf Wabe zeigend, das bei Sammlerinnen ausdrücklich einzutreten pfllegt.

Ein Protokollauszug, den wir Abb. 4, F zeigen, liefert eine einzige, doch zweifelhafte Ausnahme.

Er zeigt das Verhalten der heimkehrenden F-4, die, wie in Abb. 4, B ersichtlich, durch das Tanzen einer normalen *mellifera*-Arbeiterin, m-1Y, alarmiert, ausgeflogen war. Sofort nach Heimkehr begann dieses Individuum die Toilettebewegung. 2' nach Heimkehr suchte eine *mellifera*-Arbeiterin bei ihm nach Futter. Doch gab F-4 der Kameradin nichts und fuhr im Toilettemachen fort. 6' nach Heimkehr suchte eine *cerana*-Arbeiterin Futter bei F-4, und diesmal gab F-4 ihrem artverschiedenen Mitglied wirklich Futter ab während ungefähr 30", und ebenso nach 7' wieder einer *mellifera*-Arbeiterin während 30". Ihr Verhalten war stets sehr langsam, ohne Tanz, ohne aufgeregtes Herumkriechen auf der Wabe und ohne nochmals auszufliegen. Es scheint sehr zweifelhaft, daß jene zweimaligen Fütterungen eine eigene Sammelaktivität von F-4 bedeuten⁽¹⁾.

6. Sonstige Tätigkeiten.

Fächeln und Sterzeln wurden an verschiedenen Typen wiederholt beobachtet. Da die letztere Handlung, wie wohl bekannt, als ein Kommunikationsmittel dient, und nur von Arbeiterinnen, nicht von Drohnen ausgeübt wird, ist es beachtungswert, daß auch die Gynandromorphen von FM-, fM- u. M-Typen wiederholt sterzelten. Dabei entsprach der Grad der Ausstülpung der Nassanov'schen Drüse dem Grad des morphologischen Mosaiks. Die Individuen, die am Hinterleib weiblich sind, stülpten die Drüse wie normale Arbeiterinnen, die am Hinterleib männlichen dagegen stülpten sie nicht aus. Bei den lateralsymmetrischen Individuen war die Ausstülpung nur an der weiblichen Seite deutlich (Abb. 4, G). Das Massensterzeln wird im allgemeinen infolge der Initiative einer Arbeiterin angefangen. In der Tabelle gezeigte Daten stellen meistens ein sekundär von den anderen Genossen alarmiert entstandenes Sterzeln dar. Doch

(1) Bei den beschriebenen u. geschilderten Beispielen über Tanzfolge waren die Tänzerinnen stets *mellifera*-Arbeiterinnen, die in dieses *cerana*-Volk eingeleitet worden waren. Das bedeutet nicht immer die Unmöglichkeit der Alarmierung von *mellifera* durch den Werbetanz von *cerana*. Bei anderen normalen Arbeiterinnen beobachteten wir wiederholt die wechselseitige Alarmierung zw. dem beiden Arten und das dadurch veranlaßte Fortfliegen. Die *Sprache* dieser zwei Arten scheint demnach gegenseitig verständlich zu sein. Das möchten wir in Zukunft weiter erörtern.

gibt es darin ungefähr 10 Fälle, wobei die Gynandromorphen die Initiative ergriffen. Z. B. FM-3, die außer dem Kopf beinahe vollkommen weiblich war, ergriff manchmal die Initiative des Massenstierzels. Sogar M-5 mit dem äußerlich vollkommenen männlichen Kopf, übernahm einmal die Initiative.

Auch ist es bekannt, daß die Arbeiterinnen von *mellifera* unter Umständen stereotypisch sich mit dem Hobeln, einer schaukelnden Hin- und Herbewegung auf der Wabe, Wohnungswand u. s. w., beschäftigen (SAKAGAMI, '53 a) (1). Das wurde bei drei F-Gruppe-Gynandromorphen beobachtet. Alle diese führten sehr stereotypisch, z. B. F-4 während 20', F-2 während 28' ununterbrochen diese Handlung aus.

Die Bienenarbeiterinnen bilden oft sich zusammenkettend ein dichtes Bienennetz und decken damit den Brutbezirk. Da diese Tendenz bei *Apis i. cerana* besonders entwickelt ist, bildete unser *cerana*-Völkchen oft ein dichtes Netz. Dabei beobachteten wir viermal die Beteiligung von F-2 am Netz, in einem Fall während 2 Stunden ununterbrochen. Natürlich ist dies nicht eine aktive Handlung. Die Drohnen beteiligen sich nie darin.

Endlich kommen die Handlungen außerhalb des Stockes in Betracht. Ausfliegen in die Außenwelt (einschließlich Orientierungsflug) fand bei den meisten Individuen wiederholt statt (Tab. 1). Was die Sammeltätigkeit anbetrifft, gaben alle beobachteten Völkchen uns keine positiven Hinweise. Aber wir haben glücklicherweise das folgende Protokoll, das ganz gelegentlich von dem im Freie gelegenen Muttervolk gewonnen wurde :

Ein Individuum, Fm-2, wurde bei Heimkehr nach Pollensammeln auf dem Anflugsbrett gefangen. Die Beine dieser Biene waren an der rechten Seite vollkommen weiblich, an der linken jedoch mosaikartig. (Das einzige Individuum, bei dem in Bezug auf die Biene ein feineres Mosaik gefunden wurde.) Im rechten Pollenkörbchen trug diese Biene normalerweise ein Pollenklümpchen. Auf der Oberfläche der linken Hinterschiene, der das Pollenkörbchen fehlte, war ein kleines Pollenklümpchen angestrichen worden, das ungefähr nur 1/10-mal so groß wie das rechte Klümpchen war (Abb. 4, G).

7. Beziehung zwischen Tätigkeit und Tagesalter.

Um die Beziehung zwischen Tätigkeit und Tagesalter zu klären, wählten wir 10 Individuen, die sofort nach Ausschlüpfen in die Beobt.-Völkchen

TABELLE 3.

Das jüngste Tagesalter, in dem verschiedene Tätigkeiten zuerst beobachtet wurden.

Sg	q	G	Zp	B	Bp	W	Q	t	fan	st	fl	Hob
1-4	6-7	2-8	1-2	2-6	2	5-10	9	7-11	2-6	2-9	5-11	14

(1) Die Arbeiterin von *cerana* übt tatsächlich diese Handlung nicht aus.

eingeleitet worden waren und deren Tagesalter somit genau bestimmt werden konnte. An diesen Individuen wurde der Tag, an dem jede Handlung zuerst beobachtet wurde, in Tabelle 3 verzeichnet.

Daß manche Handlungen schon im früheren Lebensabschnitt, dagegen Wachen, Tanzfolgung und Flug etwas später erschienen, stimmt im Prinzip mit der Lebensgeschichte der normalen Arbeiterinnen überein. Ob die verschiedenen Mosaiktypen darin irgendwie voneinander abwichen oder nicht, konnten wir wegen Materialmangels nicht bestimmen.

Erörterung.

Hinsichtlich des Lebensverlaufes der gynandromorphen Bienen innerhalb eines Volkes wurde bis jetzt die folgende Meinung wiederholt ausgesprochen: Wegen ihrer Mißbildung können sie im Volk ihr Leben nicht behalten oder werden von den anderen Volksgenossen aus dem Volk herausgezerrt (z. B. ECKERT, '34, '37; MAA, '53). Natürlich könnte solche Annahme unter Umständen nicht selten zutreffen. Doch lehren unsere Ergebnisse deutlich, daß nicht alle Gynandromorphen solchem Verhängnisse unterworfen werden. Obwohl unsere Gynandromorphen nicht in den Muttervolk beobachtet, sondern künstlich in die drei Versuchsvölkchen eingeleitet wurden, konnten sogar die stark abnormen Mosaikindividuen wie FM-Gruppe sich ziemlich normal ohne Angriffen von den anderen Arbeiterinnen verhalten. Von anderen mißgebildeten Arbeiterinnen berichten HAYDAK '49 über zyklopische Bienen, und selbst ECKERT '37 über fühllose Bienen ihre ziemlich normalen Handlungen im Volk und friedlichen Beziehung zu anderen Volksgenossen.

Aus unseren Beobachtungen war zu schließen, daß manche der für Arbeiterinnen typischen Handlungen auch bei den Gynandromorphen gefunden wurden. Leider sind unsere Daten noch zu gering, um über zwei wichtigste Tätigkeiten, Brutpflege und Sammeltätigkeit genaues zu sagen. Das beruht jedoch meistens bloß auf der Kleinheit der Versuchsvölkchen. Wir glauben deshalb, daß, wenigstens in normalen Völkern, auch die Gynandromorphen, wenn sie darin produziert worden sind, mehr oder weniger sich mit beinahe allen der Arbeiterin-Tätigkeiten beschäftigen.

Unsere Daten sind allzu fragmentarisch, um zu entscheiden, ob eine quantitative Differenz in der Tätigkeitsausführung zwischen Arbeiterinnen und Gynandromorphen, sowie unter Gynandromorphen von verschiedenen Typen bestehe oder nicht. Doch dürfen wir betonen, daß sogar bei am Kopf äußerlich beinahe vollkommen männlichen Individuen einige typischen Arbeiterin-Handlungen, wie Sterzeln, Bauen, Füttern u. s. w., beobachtet wurden.

Trotz wiederholten Untersuchungen haben wir noch heute keinen positiver Nachweis bezüglich des Vorkommens des Geschlechtshormons bei Wirbellosen, das bei den Wirbeltieren aus dem Keimdrüsen sezerniert wird und auch auf die Handlungen einen merklichen Einfluß ausübt. Die

Geschlechtshandlungen der verschiedenen Gynandromorphen von *Habrobracon juglandis* beobachtend, stellte WHITING '32 fest, daß bei diesen parasitischen Wespen ihre Geschlechtshandlungen dem Kopftyp (♀ bzw. ♂) entsprechend entstehen. Daraus schloß er die ausschlaggebende Rolle des Gehirnes für die Geschlechtshandlungen der Wirbellosen, weil hierbei ein sekundärer Einfluß von den Keimdrüsen nicht der Fall ist. Daß bei unseren M-Gruppe Gynandromorphen einige, natürlich nicht primär-geschlechtliche, doch immerhin weibliche Handlungen gefunden wurden, können wir deshalb nicht sofort durch WHITING's obige Annahme erklären. Die Sachlage ist vorläufig noch zu kompliziert, um dafür eine einwandfreie Erklärung zu geben. Also möchten wir an dieser Stelle nur einige Möglichkeiten aus dem manchen denkbaren andeuten.

1. Vorkommen der weiblichen Elemente im Gehirn des äußerlich vollkommen männlichen Kopfes, obwohl sie morphologisch nicht aufweisbar sind. In diesem Fall widersprechen unsere Daten nicht der Meinung von WHITING. Unsere histologischen Beobachtungen, bei denen einige schwach weibliche Tendenzen im männlichen Gehirn gefunden wurden, steigern vielleicht die Glütigkeit dieser Annahme.

2. Vorkommen irgendeiner Quelle des Geschlechtswirkstoffes, der auch die Handlungen zum Teil beeinflußt, in der Brust od. im Hinterleib. Eine verhältnismäßig unwahrscheinliche, doch heute noch nicht völlig ausgeschlossene Möglichkeit.

3. Vorkommen irgendeiner nervösen Herrschaft über die gewissen von uns beobachteten Handlungen durch die Brust- od. Abdominalganglien. Es ist wohl bekannt, daß die Begattungshandlungen der Insekten z. Teil durch die letzten Abdominalganglien beherrscht sind (z. B. Gottesanbeterin, *Mantis religiosa*, ROEDER, '35). Natürlich ist es höchst undenkbar, daß die Brust- od. Abdominalganglien die Entstehung einer totalen Handlung beherrschen. Aber es ist nicht undenkbar, daß die gewissen Handlungen, die bei unseren Gynandromorphen beobachtet wurden, wenigstens partiell durch das Bauchmark reguliert sind, und darauf die Ueber- und Unterschlundganglien, unabhängig von der Geschlechtszugehörigkeit, eine integrierenden Wirkung ausüben.

4. Vorkommen von nichtgeschlechtlichen Elementen in den sogenannten Arbeiterin-Handlungen. In den anderen Hymenopteren nehmen die Männchen bisweilen arzeigen oder individuell an der Brutfürsorge od. den anderen weiblichen Tätigkeiten teil. Der erstere Fall ist bei einer Gruppe der Jagdwespen, Trypoxylonidae, gefunden worden. Als den letzteren Fall berichtete STEINER '32 bei einer Feldwespe, *Polistes dubia*, die eventuelle Beteiligung der Männchen an Wachen, Fächeln, Brutfüttern u. s. w. Neuerdings beobachtete Shida (1954) eine rudimentäre Trophallaxis zwischen Bruten und Männchen bei *Polistes* und *Vespula*. Deshalb ist es nicht undenkbar, daß die Anlage für gewisse als weiblich bezeichnete Handlungen auch in männlichen Individuen potentiell vorhanden sind und zuweilen verwirklicht werden. Natürlich ist die geschlechtliche Differenzierung der Honigbiene allzu stark, um sie mit

den obigen Insektenarten zu vergleichen. Aber wäre es nicht immerhin möglich, daß in den sogenannten Arbeiterin-Handlungskomplexen in ihren einzelnen Bestandteilen gewisse geschlechtsfreie Elemente enthalten sind und diese unter Umständen, besonders in Verbindung mit dem Geschlechtsmosaik, ausgelöst werden.

Unsere Daten bestehen nur aus Gelegenheitsbeobachtungen. Wenn man aber in Zukunft, wie schon von RÖSCH '28 durch Kontakt mit Kälte versucht wurde, in der künstlichen Massenerzeugung der Gynandromorphen und in ihrer systematischen Beobachtungen gewisse Erfolge erzielen könnte, so könnte man damit auf das hoch komplizierte Handlungssystem der Honigbiene wenigstens zum Teil ein Licht werfen.

Zusammenfassung.

1. Bei ungefähr 40 gynandromorphen Honigbienen (*Apis mellifera ligustica*) wurden ihre Struktur und ihre Handlungen beobachtet.

2. Sie zeigten äußerlich verschiedene Mosaiktypen. Meistenteils überwogen die männlichen Elemente am Kopf, die weiblichen dagegen am Hinterleib.

3. Das innere Mosaik im Gehirne und in den Keimdrüsen entsprach ziemlich dem der äußeren Charaktere. Aber bei einigen am Kopf äußerlich vollkommen männlichen Individuen wurde eine schwach weibliche Tendenz im Gehirn beobachtet.

4. Die in Kleinvölker eingeleiteten Gynandromorphen könnten, ohne durch die Volksgenossen hinausgezerzt zu werden, innerhalb der Völker ihr Leben behalten. Verschiedene Arbeiterin-Handlungen wurden sogar an äußerlich ♂-köpfigen Individuen beobachtet.

5. Korrelation zw. Kopftyp (♀♂) und Handlung könnte, vielleicht aus Materialmangel, nicht festgestellt werden.

6. In Bezug auf die Ausführung der ♀-Handlungen durch ♂-köpfige Individuen wurden einige Annahmen gegeben.

Summary.

1. Structure and behaviour of gynandromorphic honeybees were observed on about 40 individuals of *Apis mellifera ligustica*.

2. They showed externally various types of mosaics. In the majority, the male elements were predominant in the head, but the females in the abdomen.

3. The internal mosaics corresponded fairly well with the external ones in brain and gonads. A slight female tendency was, however, observed in the brains of certain individuals whose heads completely male-type externally.

4. When successfully introduced into other nucleus colonies, the

gynandromorphic bees could maintain their normal life in that colony, with no sign of any aggressions from other workers. Various worker-behaviours were observed even in the individuals with externally completely male head.

5. Correlation between head-type and behaviour could not be determined, perhaps due mainly to the lack of a sufficient material.

6. Some assumptions were proposed concerning performance of worker-behaviours by individuals with completely male head.

ZITIERUNG.

1950. BUTLER (C. G.), FREE (J. B.). — The behaviour of worker honey bees at the hive entrance (*Behaviour*, **4**, 262).
1934. ECKERT (J. E.). — A gynandromorphic honeybee (*J. econ. Entom.*, **27**, 1079). — 1937. Honeybee monstrosities (*Ann. entom. Soc. Amer.*, **30**, 64).
1949. HAYDAK (M. H.). — Notes on biology of cyclopic bees (*J. econ. Entom.*, **41**, 663).
1909. JONESCU (C. N.). — Vergleichende Untersuchungen über das Gehirn der Honigbiene (*Jena. Zs. Naturw.*, **45**, 111).
1952. LINDAUER (M.). — Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat (*Zs. vergl. Physiol.*, **34**, 299).
1953. MAE (T. C.). — An inquiry into the systematics of the tribus Apidini or honeybees (Hym.) (*Treubia*, **21**, 525).
1915. MEHLING (E.). — Ueber die gynandromorphen Bienen des Eugsterschen Stockes (*Verh. Physik.-med. Gesell. Würzburg*, **43**, 173).
1955. MILUM (V. G.). — Honeybee communication (*Amer. Bee J.*, **95**, 127).
1935. RÖDER (K. D.). — An experimental analysis of the sexual behaviour of the praying mantis (*Mantis religiosa* L.) (*Biol. Bull.*, **69**, 203).
1928. RÖSCH (G. A.). — Experimentelle Untersuchungen über die Entstehung von Zittern bei der Honigbiene, *Apis mellifica* L. (*Verh. Deuts. zool. Gesell.*, 1927, **219**).
1952. ROTHENBUHLER (W. C.), GOWEN (J. W.), PARK (O. W.). — Androgenesis with zygogenesis in gynandromorphic honeybees (*Apis mellifera* L.) (*Science*, **115**, 637).
1953. SAKAGAMI (SH. F.). — Untersuchungen über die Arbeitsteilung in einem Zwergvolk der Honigbiene. Beiträge zur Biologie des Bienenvolkes, *Apis mellifera* L. I (*Jap. J. Zool.*, **11**, 117). — 1954. Occurrence of an aggressive behaviour in queenless hives, with considerations on the social organization of honeybee (*Insect. Soc.*, **1**, 331).
1954. SHIDA (T.). — On the biology of a wasp, *Vespa lewisii* (Cameron) (*Lecture at 2. Ann. Meet. Japanese Section, Union intern. Etud. insect. soc. in Tokyo, in Japanese*).
1932. STEINER (A.). — Die Arbeitsteilung der Feldwespe, *Polistes dubia* K. (*Zs. vergl. Physiol.*, **17**, 101).
1955. UCHIDA (T.), SAKAGAMI (SH. F.). — The seasonal population-trends of the honey-bee in Sapporo, with some remarks on supersedure (*Jap. J. Zool.*, **11**, 55).
1932. WHITING (P. W.). — Reproductive reactions of sex mosaics of a parasitic wasp, *Habrobracon juglandis* (*J. comp. Psychol.*, **14**, 345).

SOME FACTORS AFFECTING THE SURVIVAL OF ODONTOTERMES BADIUS

W. A. SANDS, M.Sc.

(Colonial Termite Research Unit.)

INTRODUCTION

Termites of the subfamily Macrotermitinae construct within their nests sponge-like masses of comminuted wood fragments. On these grow fungi of the genus *Termitomyces*, which produce white spherical nodules about the size of a pin-head, consisting of conidiophores and conidia. These sponge-like masses are commonly known as "Fungus comb" or "Fungus gardens". The Macrotermitinae are well known in Africa and tropical Asia, as several species build large mounds which are often a conspicuous feature of the landscape.

The true relationship between the Macrotermitinae and *Termitomyces* has been the subject of discussion for many years, since the phenomenon was recorded by KÖNIG (1779) and SMEATHMAN (1781). The nature of the fungus was investigated by PETCH (1906) and the presence of spores in the gut of young termites was noted by DOFLEIN (1905). BOTTOMLEY and FULLER (1921) summarised the information available at that time, and discussed a small agaric which develops on fragments of fungus comb brought to the surface of the soil by several South African species of *Odontotermes*, which they regarded as the perfect form of the fungus of the comb, and identical with *Entolomola microcarpum* Petch, from Ceylon.

HEIM (1941 et seq.) in a series of papers, establishes the identity of the fungi associated with Macrotermitinae as belonging to the genus *Termitomyces*, and expresses the opinion that the "Fungus comb" is part of the normal architecture of the nest, and is attacked by these cavernicolous fungi simply because of its suitability as a medium.

He considers that in some cases the fungi are tolerated by the termites, in others only so long as the growth of the fungus remains within convenient limits; and that *Termitomyces* has become adapted to this particular habitat to a greater or less extent, and is not cultivated in any way by the termites.

GRASSÉ (1944) states that the termites are not known to favour the growth of *Termitomyces* by controlling other fungi such as *Xylaria*; that these are probably eliminated by the microclimate of the nest, the chemistry of the comb, and possibly by antibiotics from *Termitomyces*. He agrees (1945) with HEIM that the "Fungus comb" is "part of the architecture" and is only colonised by the fungus because of its suitability as a medium, without the intervention of the termites. He does however point out that greater or smaller quantities of spores and hyphae are found in the gut of workers and nymphs of most of the Macrotermitinae. The small quantity of fungus available prevents its use as a bulk nourishment, and he suggests that it may be a source of vitamins or similarly important substances.

GRASSÉ and NOIROT (1949) describe the nest of *Sphaerotermes sphaerotherax* (Sjöst.) and suggest that the presence of structures similar to fungus comb, which remain sterile, tends to confirm Heim's theory that the fungus is only a parasite. NOIROT (1952) discusses the theories of HEIM and GRASSÉ, and supports the view that the

fungus comb is essential to the nutrition, with the reservation that this is only in a qualitative role.

Other theories as to the function of fungus comb, apart from nutrition, have been suggested. GHIDINI (1938) considers that its function is to maintain a constant state of high humidity. LUSCHER (1951) observes that the fungus nodules are only occasionally eaten, and suggests that the fungus combs play a part in controlling nest temperature, by producing heat, possibly by bacterial fermentation, since in the case of *Sphaerotermes*, the combs bear no fungus mycelium.

METHODS AND MATERIAL

One of the greatest obstacles to any biological studies of the Macrotermitinae is the difficulty of keeping them alive under laboratory conditions. This is particularly the case in the larger species which live in colonies too large or too diffuse to permit their transference en masse to a laboratory nest. Small portions of such colonies, even when they include the royal pair, do not survive for very long, and there is no reason to suppose that their behaviour is normal during the period of dying out; any information based on mere visual observation of such fragments of colonies must necessarily be suspect on this account.

Odontotermes badius (Hav.) is a widely distributed African species, and its abundance in the vicinity of Nairobi, Kenya, where this work was carried out, made it suitable for use in a number of experiments. These are therefore only applicable to the small fungus *Termitomyces microcarpus* which is associated with this termite, but it is probable that the larger species occurring in the nests of other termite genera serve similar functions, in spite of the differences in their growth and reproductive cycles.

The experiments were extremely simple, being tests of survival under different conditions. Groups of 50 fully adult worker termites were supplied with a number of different possible food substances. Other castes were not included since these, being largely dependent upon the workers, would have introduced extra factors affecting their survival. The termites were confined in glass chambers two inches square, prepared by cementing glass strips to a glass plate with paraffin wax and closed with a loose plate laid across the top. These chambers were kept under conditions of humidity near 100 % and temperature approximately 27° C throughout the experiment. In addition to various types of food material, each group was supplied with a small quantity of moistened sterile white sand of moderately fine particle size, to enable the termites to carry on a certain amount of building activity without using the food supply for this purpose.

Each type of food material was replicated 8 or 16 times, so that in all experiments at least 400 termites were used to test one food. In experiments involving several treatments, as many as 2400 termites had to be counted out in batches of 50.

The termites were obtained by digging up large quantities of fungus

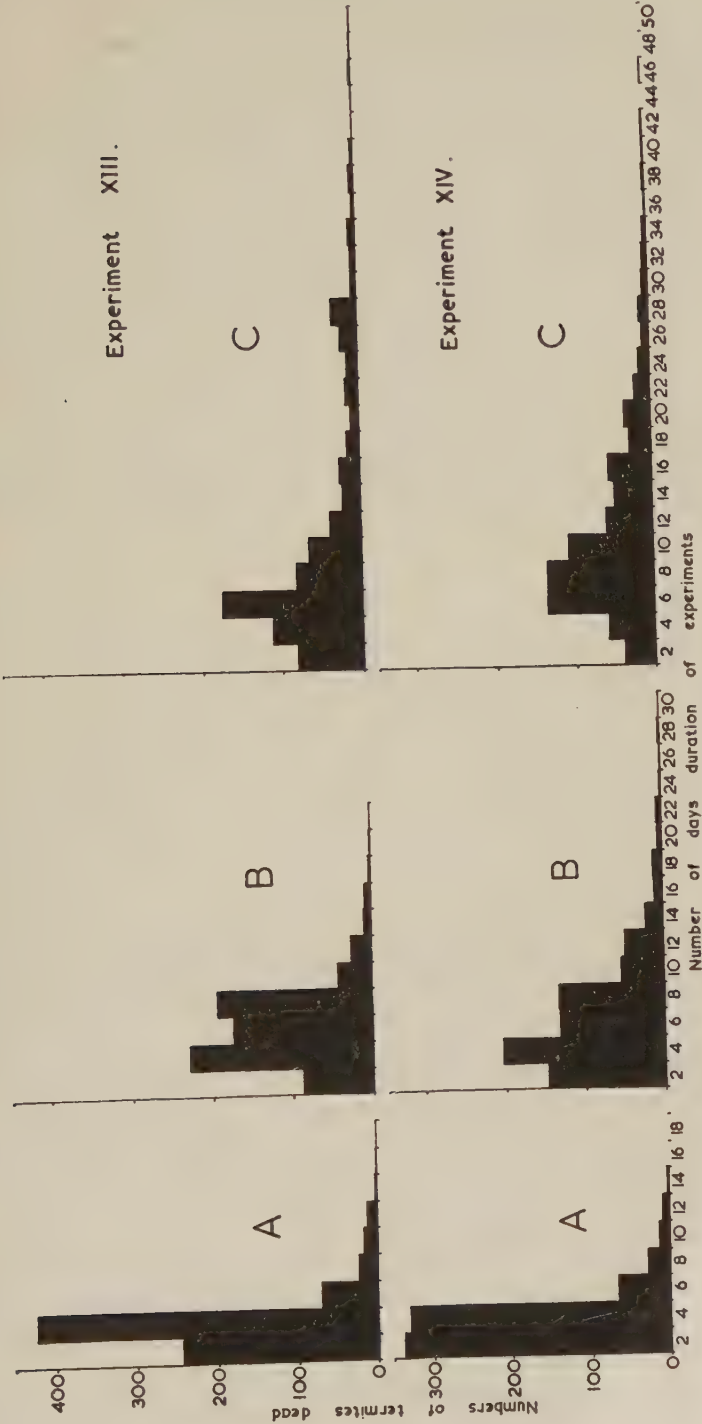


Fig. 1. — *Odontotermes badius* (Hav), A comparison of experiments XIII and XIV, showing the reduction in the number of termites dead in each 48 hour period when supplied with fungus comb. A, Complete starvation. B, Supplied with fungus comb without the nodules of conidia. C, Supplied with normal fungus comb.

comb from which all adult worker termites were extracted. The live termites were handled with brushes throughout, but in spite of this precaution all those dying in the first 24 hours of each experiment were treated as handling casualties, and replaced by live individuals. These on average amounted to about 10 % of the total number. If a similar mortality is assumed in those introduced to replace them, the final error due to handling deaths has been reduced to 1 % or less, a negligible figure, in view of a very large experimental error due to other factors — notably that of the age of the termites used. The habits of these termites are so little known that it was impossible to avoid an approximation to a normal frequency distribution of age in the samples, which to some extent masks any differences between treatments. For this reason, no result, even if statistically significant, was considered to be conclusive until it had been obtained at least twice in repeated experiments. (See fig. 1).

After the first 24 hours, dead termites were recorded daily and removed to prevent their being used as an auxiliary food supply by the survivors.

RESULTS

It was found from these experiments that when supplied with fresh fungus comb, *Odontotermes badius* workers survived for up to 55 days in the laboratory, with an average life of about 11 days. This figure of course includes all the senile specimens which are inevitably included in the experiment by virtue of the sampling method. Complete starvation produced a maximum survival of 20 days, and an average life of three days. Food materials such as wood chips, and cellulose in the form of filter paper, either enriched with starch or sugars or alone, gave similar results to complete starvation.

The only possible intermediate between these extremes was found when the termites were supplied with fungus comb from which all the nodules had been stripped. In this case the maximum life recorded was 30 days, and the average life about 6 days. When fungus comb was sterilised in an autoclave, it became useless to the termites, but this may have been due to a change making it distasteful, since the nodules of conidia were stained yellow with an infusion of the rest of the comb by this process.

Fungus comb which had been allowed to dry for some time, and had then been re-moistened and given to the termites, proved equally worthless in prolonging survival. This may again have been due to its having become distasteful, but it does otherwise suggest that the factor influencing survival may be unstable and produced by the living fungus only.

When fungus comb alone was compared experimentally with fungus comb combined with small fragments of Black Wattle (the commonest source of food in the neighbourhood), the presence of the wood chips did in some cases seem to improve longevity slightly, though the results are not conclusive.

DAY No.	CUMULATIVE TOTALS OF DEAD—AGGREGATE OF 8 SAMPLES OF TERMITES, 50 PER TREATMENT									
	Cellulose (Filter paper).		Starvation.		Dry fungus comb remoistened.		Sterilised fungus comb.		Fresh fungus comb.	
	Experiment.		Experiment.		Experiment.		Experiment.		Experiment.	
	V	VI	V	VI	V	VI	V	VI	V	VI
1	51	78	72	18	20	9	25	16	20	13
5	258	190	306	104	327	361	304	294	72	69
9	363	366	385	319	400 (Day 8)	400 (Day 6)	400 (Day 6)	400 (Day 8)	116	195
13	400 (Day 12)	398	400 (Day 10)	391					179	229
17		400 (Day 14)		400 (Day 15)					273	255
21									325	266
25									360	319
29									381	339
33									391	361
37									398	382
41									400 (Day 39)	392
45										400

TABLE 1. — *Odontotermes badius* (Hav.), a comparison of the results of experiments V and VI. Though the results were taken daily, the figures above are given at four day intervals in order to abbreviate the table to a convenient length.

Thus it appears that the *Termitomyces* found on the comb of *Odontotermes badius* produces some substance or effect which tends to promote longer survival in the termites. This factor is largely supplied by the nodules of conidia, since their removal considerably decreases the effectiveness of the comb. The fungal hyphae of the mycelium on the comb may be of some slight value in this respect, but can only be used by the termites to a limited extent, the supply presumably being quickly exhausted in the absence of the nodules. It has also been observed during the course of these experiments that if *Odontotermes* workers are deprived of fungus comb for several days, and then allowed access to it, their first reaction is to consume rapidly a number of nodules of conidia. If these are in limited supply, the portion of comb may be entirely stripped in a short time.

DISCUSSION

It seems that though the fungus *Termitomyces microcarpus* may not in itself be sufficient to support life in *Odontotermes badius* for prolonged

periods, it is extremely important to the termites, since without it they are unable to survive any longer than they do when completely starved. The function suggested by GRASSÉ and NOIROT (1944), namely that the fungus is a source of vitamins or similar essential substances, may well be correct. If, as HEIM (1941 et seq.) suggests, the fungus were only a cavernicolous form making use of a suitable medium, and tolerated by the termites, it would be hard to explain the marked effect it shows on termite survival. This may have been the state of affairs at some period during the evolution of both *Termitomyces* and the Macrotermitinae, but the relationship between them now appears to be one of symbiosis.

REFERENCES

1921. BOTTOMLEY (A. M.), FULLER (C.). — The fungus food of certain Termites (*S. Afr. J. nat. Hist.*, **3**, 139-44 et 223).
 1938. GHIDINI (G. M.). — La presumibile funzione delle spugne legnose nei nidi dei Metatermitidi (*Riv. Biol. colon.*, **1261**, 261-267). — 1941. A proposito di alcune recenti ricerche (*Boll. Zool. Turin*, **12**, 113).
 1944. GRASSÉ (P. P.). — Recherches sur la Biologie des Termites champignonnistes (Macrotermitinae) (*Ann. Sci. nat. Paris*, II, **6**, 97-171). — 1949. Recherches sur la Biologie des Termites champignonnistes (Macrotermitinae) (*Ibid.*, **7**, 115-146).
 1949. GRASSÉ (P. P.), NOIROT (C.). — Sur le nid et la Biologie du constructeur de meules sans champignons (*Ann. Sci. nat., Paris*, II, **10**, 149-166). — 1951. Nouvelles recherches sur la Biologie de divers Termites Champignonnistes (*Ann. Sci. nat., Paris*, II, **13**, 291-342).
 1940. HEIM (R.). — Études descriptives et Experimentales sur les Agarics Termitophiles d'Afrique Tropicale (*Mem. Acad. Sci., Paris*, **64**, 1-74). — 1942. Les Champignons des Termites (*Rev. Sci., Paris*, **80**, 69-86). — 1950. Un *Termitomyces* sur meules d'un *Ancistrotermes* Africain (*Rev. Sci., Paris*, **88**, 3-13). — 1952. Classement Raisonné des Parasites Symbiotes, Commensaux et Saprophytes d'origine fongique associés aux termites (*VI Congreso Internacional de patologia comparada*, Madrid, 4-11 Mayo, 1952). — 1952. Les *Termitomyces* du Cameroun et du Congo Français (*Denkschr. schweiz. naturf. Ges.*, **80**, 1-29).
 1951. LUSCHER (M.). — Significance of fungus gardens in termite nests (*Nature, Lond.*, **137**, 34).
 1952. NOIROT (C.). — Les soins et l'alimentation des jeunes chez les Termites (*Ann. Sci. nat., Paris*, II, **14**, 405-414).
-

THE FORAGING BEHAVIOR OF HONEYBEES ON HAIRY VETCH

FORAGING METHODS AND LEARNING TO FORAGE (I)

by

NEVIN WEAVER

(Texas Agricultural Experiment Station, College Station, Texas, U. S. A.)

The foraging behavior of honeybees is a product of the interaction between bees and the plants foraged. Since both are variable, foraging statistics are likely to be inconclusive, or to apply only to the particular case under study. Observations of larger populations under varying conditions may be of more value in making fruitful generalizations than more limited quantitative data; such observations are also necessary as a guide to the adequacy of data derived from smaller samples. Generalizations that are not supported by adequate data, on the other hand, must be viewed with suspicion and often the data itself will indicate aspects of behavior which were not discerned during general observations.

MATERIALS AND METHODS

In 1953, 1954, and 1955 studies were conducted on the behavior of honeybees (*Apis mellifera* L.) foraging from hairy vetch (*Vicia villosa* Roth.). The observations were made near Terrell, Texas, U. S. A., the main vetch seed producing area of the state. Most of the observations in any one year were made in the same vetch field. A majority of the bees were of the Italian race, though some were mixtures of two or more races.

During this study measured or estimated one square yard areas were used for several purposes. These are reported below as one square meter areas since, in the manner in which they are used, this does not vitiate the data. Weights taken in pounds have been converted to kilograms.

The amount of bloom was estimated weekly from the number of open, unwithered blossoms in 1 square meter of vetch without skips between the vines. The number of foragers was determined by staking off five one square meter areas and counting the number of bees working in the areas on different days and at different times of the day. For estimates of the number of foragers in other fields, or in other parts of the same field, the number of bees working in an estimated one square meter area was counted, and then the observer moved three paces and made another count.

A colony of bees on scales was used to measure the nectar flow. The daily nectar flow was determined as the gain in weight of the colony from early morning before flight began to late afternoon when it had ceased. In 1955 the amount of nectar available in the blossoms was measured by the centrifuge method of SWANSON and

SHUEL (1950). The concentration of nectar from the honey stomachs of bees was determined daily between 1300 and 1600 hours with a hand refractometer; the mean of at least two uncorrected readings was considered to be the sugar concentration. Details of these techniques, of the culture, blooming period, nectar flow, and pollination, of the vetch are published elsewhere (WEAVER, 1956 *a*).

The proportion of foragers of each of two general types was determined by observing the foraging method of all bees immediately in front of the observer, moving three paces, and making another count of the bees of each type. This was continued until a predetermined number of bees had been observed. If more information on each bee was needed, the pertinent information was gathered on only the first bee that came into view at any one place, then the observer moved three paces to gather information on another bee.

To determine the amount of forage gathered by a bee on one foraging trip, bees returning from the field were caught at the hive entrance; the honey stomach was removed and weighed with its contents to the nearest 1 mg. The weight of the two pollen pellets was also determined to the same accuracy.

Data were analyzed statistically by the χ^2 test or by the method of paired differences. These methods, as well as the method of determining the correlation coefficient, are taken from SNEDECOR (1946).

RESULTS

A honeybee must insert her tongue to the base of the corolla tube in order to reach the nectary, and if she approaches the blossom from the mouth she must trip the blossom, depress the keel, and force her head into the corolla tube. Both tripping the blossom and reaching the nectar are difficult for a honeybee. The tongue is inserted into the blossom between the keel and the standard and is thrust sharply toward the base of the corolla tube. The head is then used as a wedge and lever while the legs press downward on the keel. The sexual column of vetch, unlike that of alfalfa, usually is not released with a snap, but the bee's tongue is sometimes caught between the sexual column and the standard, and occasionally there is a short struggle before it is pulled free. The head usually is twisted to one side when the blossom trips and the position of the tongue apparently determines whether or not it is caught; some bees got their tongues caught in almost every blossom, others almost never. The bee depresses the keel to at least a right angle with the corolla tube and clings to it as she thrusts her tongue to the nectary on the dorsal side of the sexual column at its base. A bee can also reach the nectary without tripping the blossom by inserting her tongue between the petals of the standard and the keel at the base of the corolla tube. Most of the bees that work in this manner alight on the ventral side of the blossom facing the axis, but some bees usually face at almost a right angle to the corolla tube, and there may be some variation in the position of a bee foraging successive blossoms. The position depends, in part, upon the direction from which the bee approaches the blossom. In order to avoid confusion, all bees that trip the blossoms will be called trippers, and all non-trippers that reach the nectar by inserting the tongue between the petals will be called base workers.

In order to study the process by which the foraging method became fixed, colonies of bees that had never worked vetch were moved, one at a time, into a field with a good nectar flow and a low population of foragers. After three or four hours with little flight from the colony, there would be a sudden burst of activity and the vetch near the hive would be filled with bees that appeared frantic in their efforts to forage from the blossoms. Some bees made no real effort to forage from any blossom that had not previously been tripped. Others would alight and randomly attempt to insert the tongue into a blossom at any point; a bee that had succeeded in foraging from one blossom as a base worker might alight on the dorsal side of the next flower and attempt to insert the tongue; a bee would often insert the tongue between two contacting blossoms, or against a standard or keel of a previously tripped blossom, and thrust the head sharply downward in a typical tripping motion. Upon successfully working one blossom, or a very few blossoms in succession, most bees immediately became oriented in their behavior patterns, and calmly and methodically foraged from additional flowers by whatever method had proved successful. This change in the approach to foraging sometimes was gradual, but it usually was quite sharp and dramatic. Before they learned their foraging method the bees were so nervous in their actions and flew great distances so often that none was observed from the time she arrived in the field until she established her foraging method, so it is not known how many successful visits may have occurred before the foraging method was learned. One bee, however, was followed while she visited well over a hundred blossoms and finally returned to the hive without becoming oriented in her foraging behavior. This bee successfully foraged from 34 blossoms as a base worker, 23 blossoms as a tripper with the tongue entering the blossom on the right side of sexual column, and 14 blossoms as a tripper entering to the left; 32 unsuccessful attempts to work blossoms were recorded, and many other unsuccessful or indecisive visits occurred in such rapid succession that no records were made. Several times this bee succeeded in working several successive blossoms by one method, and began approaching each blossom in the same manner and acting less nervous, but a failure would be followed by more disorganized activity. These results are in agreement with those of Reinhard (1952) who studied bees learning to forage from alfalfa blossoms, but the studies need to be extended in order to gain knowledge of the latent period of learning of bees, the effect of experience at foraging from other types of blossoms on the time required to learn to forage medium sized papilionaceous blossoms, and individual and colony differences in learning ability.

Random observations indicated that, after the bees' foraging methods had become established, the percentage of base workers varied with the condition of the vetch plants. In 1954 a series of five paired observations on the number of tripping bees per 100 foragers in areas of a field with scattered blossoms and in areas of the same field with numerous blossoms was therefore undertaken. These data are given in Table 1. In an experi-

ment on the control of destructive insects of vetch the check plots became rather heavily infested with pea aphids and showed slight thrips damage (Weaver and Garner, 1955). On five occasions the number of trippers per 25 bees was counted in a plot in which aphids and thrips were controlled and in a check plot in which they were not. Since there were approximately equal numbers of blossoms in the insect infected and check plots, the number of foragers in 10 randomly selected estimated 1 square meter areas in each plot was also determined on five occasions. Table 1 gives the data on the number of trippers and the pooled data on the number of bees in

TABLE 1. — Paired counts of the proportion of tripping honeybees, and the number of foraging honeybees in hairy vetch under the conditions indicated.

TRIPPERS PER 100 BEES.		TRIPPERS PER 25 BEES.		BEES IN 10 SQ. METERS.	
Numerous blossoms.	Scattered blossoms.	Insects controlled.	Insects not controlled.	Insects controlled.	Insects not controlled.
80	51	20	13	9	7
77	36	13	9	4	2
85	60	17	13	19	10
82	46	16	12	13	5
66	30	22	14	16	21
Means.		Means.		Means.	
78.0	44.6	17.6	12.2	12.2	9.0
t = 11.93 **		t = 6.21 *		t = 1.28	

* Probability < 0.01.

10 square meter areas. The mean difference in the proportion of trippers was highly significant in both sets of data, but the mean difference in the number of foragers was not significant. In fields with a few clumps of vigorous vetch surrounded by weak plants, the increased proportion of trippers in the better vetch was obvious. Similarly, in 1954 fields with vigorous appearing vetch always had a higher percentage of trippers than fields of weak vetch. Observations late in the season in 1955 were similar to those in 1954, but those early in the season were not. Since there was no objective method of measuring the vigor of plants, these conclusions are based on many brief observations; little data were gathered and none are presented.

The primary classification of bees was as trippers or base workers, but for some purposes the trippers were divided into 3 classes according to forage gathered, and into 3 classes according to foraging method. The complete classification according to forage gathered was as follows: (1) Pollen gatherers: bees that foraged only in the mouth of the blossom for pollen; (2) Pollen and nectar gatherers: tripping bees that extended the tongue into

the blossom to the nectary, and that had pollen visible on the corbiculae; (3) Nectar gatherers: bees behaving like (2) but with no pollen visible on the corbiculae; (4) Base workers. The complete classification according to foraging method was as follows: (1) Pollen gatherers; (2) Trippers reaching the nectary by inserting the tongue into the blossom to their right, or (3) To their left of the sexual column; (4) Base Workers; (5) Mixed: bees working some blossoms as trippers and others as base workers. Because the systems overlap, there is a total of 7 classes.

On each of six occasions during 1955, 50 bees were observed while working two to ten blossoms and then were classified according to foraging method and forage gathered. The number of bees in each classification is given in Table 2. Similar but less extensive data were obtained in 1953 and 1954. There were never many bees that foraged alternately as trippers and base workers; this was particularly true in 1954. Most of the bees that did mix their methods attempted to trip all blossoms, but if one did not trip easily, the bee changed positions and foraged as a base worker; a few bees, especially late in the season, foraged most blossoms as base workers but inserted the tongue into the mouth of some of the previously tripped blossoms. The number of bees foraging for pollen only was always small, but the number of bees in most of the other classes was quite variable and some of this variability could be related to the nectar flow. From May 5 to May 10, 1955 the amount of nectar brought into a colony each day diminished from 10 to 6 kg; on May 12 the colony stored $2\frac{1}{2}$ kg; and there after never more than $\frac{1}{2}$ kg in a day. After several days with a poor nectar flow the percentage of trippers gathering nectar only fell sharply, the percentage of trippers gathering both nectar and pollen increased slightly, and the percentage of base workers increased sharply. This can be seen for 1955 from the data in Table 2. The nectar flow and the proportion of each type of forager on the first and last observations in 1953 were almost identical with the corresponding data in 1955. In 1954 when the nectar flow was slow throughout the year, there were never many trippers gathering nectar only, and the percentage of base workers was high all season long. The slight increase in the proportion of bees with pollen visible on the corbiculae during the slow nectar flow may have been due to the longer time required for a bee to gather a load, and the consequent reduction in observations on bees that had just arrived in the field, but prolonged observations on a large number of foragers during the three years established the reality of the change in the proportions of base workers and trippers gathering nectar only.

Although a large proportion of the trippers gathered both nectar and pollen, few of them foraged specifically for pollen. When the blossoms were tripped the anthers hit the head or thorax of most bees, and varying amounts of the pollen that clung to the bees was packed on the corbiculae; nectar gathering trippers would sometimes cleanse the body of pollen, but not pack it.

On two days, when the colony on scales gained 0.5 and 1.6 kg of

nectar containing 40 per cent sugar, returning foragers were caught at the hive entrance and their forage was removed and weighed. Thirty-two bees with pollen on the corbiculae carried 4.5 ± 0.5 mg of pollen and 14.7 ± 1.3 mg of nectar; the amount of pollen and nectar carried by individual bees was not correlated ($r = 0.088$). Eight bees without pollen carried 19.8 ± 2.7 mg of nectar. One of these bees, with 9 mg of nectar, had pollen on the pollen brushes and on the under side of the head. This bee was probably a tripper, and the remaining bees without pollen were probably base workers. The loads carried by these bees were small in comparison to the loads recorded from other species of plants (eg. Park, 1922). Visual observations indicated that bees gathering only pollen from vetch usually gathered larger loads than any which were weighed in this series, and that during a better honey flow more nectar was carried per load by both trippers and base workers. Analytical balances were not available in the field at other times.

TABLE 2. — Number of honeybees using foraging method and gathering forage as indicated from hairy vetch on 6 occasions in 1955.

DATE.	TIME.	TRIPPERS.				Pollen only.	Base workers.	Mixed method (4)	TOTAL No. bees.
		Nectar only (1).		Nectar and pollen (2)					
		Right (3)	Left (3)	Right (3)	Left (3)				
5/5	1100	15	8	10	10	1	2	4	50
5/5	1530	9	8	10	10	1	9	3	50
5/7	0830	16	7	14	5	2	6	0	50
5/7	1100	15	6	11	7	4	7	0	50
5/12	1330	8	7	14	11	1	8	1	50
5/17	1100	2	3	16	8	1	18	2	50
Total.		65	39	75	51	10	50	10	300

(1) No pollen visible on corbiculae.
(2) Foraging for nectar and with pollen on corbiculae.
(3) Inserting tongue into blossom to the right or the left of the sexual column.
(4) Foraging some blossoms as trippers and others as base workers.

Of the trippers that gathered some nectar, 59 per cent inserted the tongue to the right of the sexual column, and 41 per cent to the left. As can be seen from the part of the data which is shown in Table 2, there was considerable variation from one count to the next, but the proportion departed significantly from both a 1:1 and 2:1 ration by the X^2 test. Bees that were oriented in their foraging behavior were more constant in inserting the tongue into the same side of the blossom than in foraging exclusively as trippers or base workers. The direction of foraging became fixed while the

bees were learning to forage, so it would seem that there is an innate tendency for bees to enter the blossom from one direction or the other, or there is an asymmetry in the vetch blossom not visible to the human eye.

DISCUSSION

One of the more useful concepts of foraging behavior is that the relative attractiveness of a source of forage depends upon a balance between the factors that attract bees and those that repel them. For an interpretation of some of the results obtained in this study a more specific concept would be useful. Experiments by von FRISCH (1923, 1934, 1942), WYKES (1952), BEUTLER (1950), and LINDAUER (1949) demonstrated that bees prefer certain sugars to others of the same concentration; that bees prefer high concentrations of any attractive sugar to low concentrations of the same sugar; and that the preferences are determined by the sense of taste, the sense of smell, and other physiological factors. Among these factors is the time, energy, or bother required to gather a load. Bees feeding on dishes abundantly supplied with sugar syrup gathered larger loads, gathered loads more quickly, danced more vigorously, and attracted more recruits than bees fed on a thin film of syrup of the same concentration that had to be sucked from blotting paper (von FRISCH, 1923).

It is postulated that, all else being equal, honeybees will gather nectar which yields the greatest amount of sugar (potential energy) per unit expenditure of energy, and that when the amount of sugar gathered becomes too low in relations to the amount of energy expended, the bee will either cease to forage or seek a new source of forage. It is not assumed that the bees perceive the food value of the sugars *per se*, but only the taste and other characteristics of the solution. There are, of course, many factors which influence a bee's selection of and adherence to a source of forage (RIBBANDS, 1949, 1953), and the other factors will affect the ratio of incoming to outgoing energy required by each individual to cause a change in foraging.

The blossoms of hairy vetch are difficult for a honeybee to forage, and the fact that during a poor nectar flow bees returned to the hive with small loads of nectar can be explained by the assumption that the return in forage was not sufficiently large in relation to the energy expended in gathering it to cause bees to continue to forage on that particular trip to the field. Alternate explanations would be that bees will expend only a limited amount of energy or will forage for only a limited amount of time regardless of the richness of the forage.

The decrease, during poor nectar flows, in the proportion of trippers gathering nectar only while the proportion gathering both nectar and pollen remained almost constant can be similarly explained. A greater return of forage per blossom and per unit expenditure of energy is obtained by the bees gathering both. The need of the colony for pollen probably helped

to cause some bees to gather both pollen and nectar, especially since there was no other good source of pollen available to the bees, and the few bees foraging for pollen only probably had to trip about 200 vetch blossoms in order to gather a load.

Data on the foraging speed of bees indicate that base workers forage about 90 more blossoms per hour than tripping nectar gatherers (WEAVER, 1956 *b*). Furthermore, base workers did not appear to expend nearly so much muscular energy in reaching the nectar as trippers. This was particularly true in 1954 when the vetch blossoms were more difficult for the bees to trip than in 1953 or 1955 (WEAVER, 1956 *b*). Both the difficulty of tripping the blossoms and the small return in nectar could have contributed to causing the large proportion of base workers in the vetch throughout 1954 and late in 1953 and 1955. The field of vetch that lacked vigor and had many trippers early in 1955 had little nectar available in the blossoms, but the blossoms looked weak and were quickly and easily tripped, so it is possible that there was little difference in the amount of energy expended by trippers and base workers in that field.

The data taken in 1954 and summarized in Table 1 can also be explained on the basis of energy relations. It would be expected that vetch heavily infested with aphids would secrete less nectar than uninfested vetch. Moderate numbers of thrips would not be expected to affect nectar secretion, but might make the vetch less attractive to bees in other ways; foragers appeared to be irritated by thrips that mounted their bodies. Scattered bloom would be less attractive to bees than crowded blossoms both because of the flight distance between racemes and the searching time required. The same factors which resulted in scattered bloom might also have caused poorer nectar yield by the blossoms. This was probably the case during these observations, since the vetch with scattered blossoms was maturing many seed, and this seems to reduce the amount of nectar secreted (WEAVER, 1956 *a*).

Regardless of the cause of the change in the proportions of trippers and base workers when the nectar flow deteriorates, the mechanism of the change is not at all clear. All of several possible mechanisms may operate to some extent. Observations at the hive entrance and hourly weighings of the colony on scales indicated that a smaller percentage of the colony population was going into the field late in 1953 and 1955 than early in those seasons. If more base workers than trippers continued to forage, this could account the change in the proportions of the two types of foragers as the nectar flow deteriorated.

The data in Table 1 indicates that there were probably fewer foragers in the plot being attacked by aphids than in the plot in which insects were controlled, though the differences were not great enough to be statistically significant. Some of the bees that originally foraged in the infested plot may have quit foraging or they may have changed foraging areas. The evidence indicates that bees are sometimes recruited to a new foraging area in a different field from their old one (WEAVER, 1956 *a*, 1956 *b*). A bee

might also wander into a more satisfactory part of the field since, during a poor nectar flow, bees explore and forage over a wider area than during a good flow.

Competing foragers are important in making bees move about more, both by their physical presence and by removing nectar from the blossoms and thus making the vetch less attractive (WEAVER, 1956 *b*). A tripper's eyes and antennae are partially covered while her head is pushed into the blossom to reach the nectary, but the base worker's eyes and antennae are fully exposed at all times. During prolonged observations on the foraging behavior of individual bees it was noted that base workers appeared to be disturbed more than trippers by the presence of an observer, and several observations indicated that they also might be more sensitive than trippers to the presence of competing foragers; they seemed more prone than trippers to take evasive action when another forager flew fairly close, and often visited a raceme deep in encircling vines, or flew away from the area after such evasive actions. A greater sensitivity to competing foragers would tend to force a bee into an area with less competition. Objective data on the distance of flights by trippers and base workers (WEAVER, 1956 *b*) and on the exposure of the racemes preferred by these types of foragers failed to indicate clearly whether or not trippers and base workers differ in these respects. The techniques available for these studies were either too insensitive to demonstrate any differences that might have occurred, or depended upon subjective decisions by the observer.

It was considered possible that some bees might begin foraging as trippers and change to base workers after the foraging method had been established. The fact that up to eight per cent of the apparently oriented bees observed foraging from only 2 to 10 blossoms worked as both trippers and base workers indicated that tripping bees with some experience as base workers were fairly numerous. It may be that some of these bees changed completely to the base working habit as their experience increased or as the nectar flow deteriorated. This conclusion is supported by the fact that in 1954 when the blossoms were difficult to trip (WEAVER, 1956 *b*) only one bee was observed to forage alternately as a tripper and base worker.

There is also opportunity for a bee that has never foraged except as a tripper accidentally to learn to forage as a base worker. In attempting to trip a blossom, a bee's tongue often slips down the side of the corolla tube between the petals of the standard and the keel. Instead of reaching the nectary from this position, all the bees observed, except one bee visiting one blossom, withdrew the tongue immediately and again attempted to trip the blossom. Several random observations, however, indicated that the base working habit may sometimes have been acquired in this manner. A few bees inserted the tongue at the mouth of the blossom, pushed the head far to the side and reached the nectary from the position normal to trippers, but without tripping the blossom. Others inserted the tongue in the same way, but then moved around and down the corolla tube while the tongue was in the blossom, and reached the nectary from the normal

position of base workers. One of these bees tripped over half of the blossoms before changing positions and foraging as a base worker.

It is believed that most of the trippers that had some experience as base workers, and possibly a few others, changed to base workers as the nectar flow deteriorated, that most of the nectar gathering trippers that did not make this change began foraging for both nectar and pollen or ceased to forage, and that different environmental factors influence trippers and base workers differently in causing them to change their foraging areas.

Summary.

The honeybee can reach the nectar from the mouth of the hairy vetch blossom by tripping it, or she can insert her tongue between the petals at the base of the corolla tube and reach the nectar. These non-trippers are called base workers. The foraging method is learned and becomes fixed through success at foraging from a very few blossoms in one manner during almost random attempts to reach the nectar. A slightly larger percentage of trippers reached the nectar by inserting the tongue to their right than to their left of the sexual column. There were never many bees in the field that foraged some blossoms as trippers and others as base workers, nor were there many that foraged for pollen only. When there was a good nectar flow early in the season there were few bees foraging as base workers, and the number of trippers foraging for nectar only was about equal to the number gathering both pollen and nectar. After a few days with a poor nectar flow the percentage of tripping bees gathering nectar only decreased sharply, the percentage gathering both nectar and pollen increased slightly, and the percentage of base workers increased sharply. There was a larger proportion of base workers in vetch with scattered blossoms than in vetch with numerous blossoms, and also a larger proportion of base workers in vetch with a heavy aphid infestation than in vetch in which these insects were controlled. During a poor nectar flow base worker gathered larger loads of nectar than trippers. To explain these observations, it is proposed that bees prefer to gather nectar which yields the greatest return in sugar per unit expenditure of energy, and that base workers expend less energy in foraging from blossoms than trippers. It is believed that base workers are more sensitive than trippers to competing foragers, and thus are more likely to be forced into areas with the least competition, that as the nectar flow deteriorates more trippers than base workers cease to forage, and that most of the bees that normally trip blossoms but have had some experience as base workers, and possibly some other trippers, begin to forage exclusively as base workers.

Sommaire.

L'Abeille peut atteindre par la bouche le nectar de la fleur de la vesce velue (*Vicia villosa*) en la " tripping " ou elle peut insérer la langue entre

les pétales à la base de la corolle et ainsi atteindre le nectar. Ces Abeilles "non-tripping" s'appellent les ouvrières de base. Cette méthode de butiner est apprise et devient fixe à cause du succès à butiner une petite quantité de fleurs d'une seule façon pendant pour ainsi dire des essais d'atteindre le nectar à l'aventure. Un pourcentage plus grand de "trippers" ont atteint le nectar en insérant la langue à droite de la colonne sexuelle que celles qui l'ont insérée à gauche. Il n'y avait jamais beaucoup d'Abeilles dans le champ qui butinaient les fleurs tantôt comme "trippers", tantôt comme ouvrières de base. Il n'y avait pas non plus beaucoup d'Abeilles qui butinaient le pollen uniquement. Quand il y avait une bonne miellée dans la première partie de la saison, il y avait peu d'Abeilles butinant comme ouvrières de base, et le nombre d'Abeilles "tripping" butinant le nectar uniquement était à peu près égal au nombre recueillant et le nectar et le pollen. Après quelques jours d'une miellée pauvre, le pourcentage des Abeilles "tripping" recueillant le nectar uniquement diminuait nettement, le pourcentage des Abeilles recueillant et le nectar et le pollen augmentait un peu, et le pourcentage des ouvrières de base augmentait nettement. Il y avait une plus grande proportion d'ouvrières de base dans la vesce aux fleurs dispersées que dans la vesce aux nombreuses fleurs, et aussi une plus grande proportion d'ouvrières de base dans la vesce infestée d'Aphides que dans la vesce dans laquelle les insectes étaient maîtrisés. Pendant une miellée pauvre, les ouvrières de base ont recueilli de plus grandes quantités de nectar que les "trippers". Pour expliquer ces observations, il pense que les Abeilles aiment mieux recueillir le nectar qui donne le plus grand renvoi de sucre par unité d'énergie dépensée et que les ouvrières de base dépensent moins d'énergie à butiner les fleurs que les "trippers". Je crois que les ouvrières de base sont plus sensibles que les "trippers" à la concurrence des autres butineuses et, donc, peuvent être plus facilement obligées d'aller dans les sections moins compétitives, que plus de "trippers" que d'ouvrières de base cessent de butiner quand la miellée s'amenuise, et que la plupart des Abeilles qui "trip" les fleurs habituellement, mais qui ont un peu d'expérience comme ouvrières de base, et, probablement quelques autres "trippers", commencent à butiner exclusivement comme ouvrières de base.

Zusammenfassung.

Die Honigbiene kann vom Munde der behaarten rauhaarigen Wickenblüte (*Vicia villosa*) aus an den Nektar kommen, indem sie die Blüte oben aufschnellen läßt, oder sie kann den Rüssel, zwischen den Blütenblättern am unteren Ende der Korollenröhre hindurchzwängen und so den Nektar erreichen. Diese Blüten nicht schnellenden öffnenden Arbeitsbienen nennt man Bodenarbeiterinnen. Die Sammelmethode wird erlernt und beibehalten durch erfolgreiches Sammeln nach derselben Methode an einigen wenigen Blüten bei fast planlosen Versuchen, den Nektar zu erreichen Ein

etwas größerer Prozentsatz von blutenschnellenden Bienen erreichten den Nektar, indem sie den Rüssel rechts statt links an dem Stempel vorbeizwängten. Es gab nur wenige Bienen im Felde, die einige Blüten als Schnellerinnen, andere Blüten dagegen als Bodenarbeiterinnen besuchten; auch waren nicht viele da, die nur Pollen einsammelten. Bei reichlicher Nektartracht im Frühjahr gab es nur wenige Bodensammlerinnen, und die Anzahl von Schnellerinnen, die nur Nektar sammelten, war etwa der Anzahl derer gleich, die sowohl Nektar als auch Pollen sammelten. Nach ein paar Tagen mit schlechtem Nektarertrag ging der Prozentsatz von schnellenden Nur-Nektar-Sammlerinnen stark zurück; der Prozentsatz von Bienen, die zugleich Nektar und Pollen sammelten, nahm um ein wenig zu; und der Prozentsatz von Bodensammlerinnen erfuhr eine starke Erhöhung. Es wurden mehr Bodensammlerinnen in Wicken mit verstreuten Blüten festgestellt als in denen mit zahlreichen Blüten. Dasselbe gilt für Wicken, die stark mit Blattläusen verseucht sind, gegenüber solchen worin die Schädlinge im Zaum gehalten werden. Wenn wenig Nektar erzeugt wird, sammeln die Bodensammlerinnen mehr Nektar als die Schnellerinnen. Um diese Beobachtungen zu deuten, folgern wir so: die Bienen sammeln am liebsten da, wo die größte Ausbeute an Zucker je Einheit Energieverbrauch zu erzielen ist, und die Bodensammlerinnen verbrauchen weniger Energie beim Besuch der Blüten als die Schnellerinnen. Man glaubt weiter, daß die Bodenarbeiterinnen konkurrierenden Insekten gegenüber empfindlicher als die Schnellerinnen seien, und daß sie so mit größerer Häufigkeit gezwungen werden, Gebiete mit wenigern Konkurrenten zu besuchen; daß wenn die Tracht versiegt, mehr Schnellerinnen als Bodenarbeiterinnen zu sammeln aufhören, und daß die meisten Bienen, die normalerweise zu den Schnellerinnen gehören, aber außerdem etwas Erfahrung als Bodenarbeiterinnen haben (und vielleicht auch einige andere Schnellerinnen) jetzt ausschließlich als Bodenarbeiterinnen zu sammeln anfangen.

REFERENCES CITED

1951. BEUTLER (R.). — Time and distance in the life of the foraging bee (*Bee World*, **32**, 25-27).
 1923. FRISCH (K. von). — Ueber die "Sprache" der Bienen. Ein Tierpsychologische Untersuchung (*Zool. Jahrb. Abt.*, **340**, 1-186). — 1934. Ueber den Geschmackssinn der Biene. Eine Beitrag zur vergleichenden Physiologie des Geschmacks (*A. vergl. Physiol.*, **21**, 1-156). — 1942. Die Werbetänze der Bienen und ihre Auslösung (*Naturwissenschaften*, **30**, 269-277).
 1949. LINDAUER (M.). — Ueber die Einwirkung von Duft- und Geschmacksstoffen sowie anderer Faktoren auf die Tänze der Bienen (*A. vergl. Physiol.*, **31**, 348-412).
 1922. PARK (O. W.). — Time and labor factors involved in gathering pollen and nectar (*Amer. Bee Jour.*, **62**, 254-255).
 1952. REINHARDT (J. F.). — Some responses of honeybees to alfalfa flowers (*Amer. Nat.*, **86**, 47-66).
 1949. RIBBANDS (C. R.). — The foraging method of individual honeybees (*Jour. Anim.*

- Ecol.*, **18**, 47-66). — 1953. The behavior and social life of honeybees (*London: Bee Research Assn.*, 352 p.).
1946. SNEDECOR (G. W.). — Statistical methods (*4th Ed. Ames, Iowa State Col. Press*, 485 p.).
1950. SWANSON (C. A.), SHUEL (R. W.). — The centrifuge method for measuring nectar yield (*Plant Physiol.*, **25**, 513-520).
- 1956 a. WEAVER (N.). — The pollination of hairy vetch by honeybees (*Jour. Econ. Ent.*, In Press). — 1956 b. Foraging behavior of honeybees on hairy vetch. II. Foraging areas and foraging speed (*Insectes sociaux*, In Press).
1955. WEAVER (N.), GARNER (C. F.). — Control of insects on hairy vetch (*Jour. Econ. Ent.*, **48**, 625-626).
-

II

NOUVELLES DE L'UNION

TRAVAUX PUBLIÉS PAR LES MEMBRES DE L'UNION

MILNE (P. S.). — 1945. **Sulphonamides and American foul brood disease of bees.** (*Nature*, **155**, 335.)

In 1944, Prof. Haseman of the University of Missouri, Columbia, reported that sugar syrup containing sulphathiazole fed to bees enabled them to raise healthy brood in combs containing the "scales" of larvae which had died of American Foul Brood. In 1943 a beekeeper, Mr. Ekins of Surrey, claimed to have obtained similar results with sulphapyridine. Trials, with sulphapyridine for the elimination of A. F. B. from colonies of bees, carried out at Rothamsted in 1944, yielded promising but not conclusive results. It appeared that during the course of treatment, progress of the disease within the colony was arrested, and that only healthy brood was being reared in combs where the disease had previously been established.

MILNE (P. S.). — 1947. **Sulphonamides and A. F. B.** (*Progress Report. Agriculture.*)

Experiments were conducted during 1946 in collaboration with County Beekeeping Instructors and Bee Disease Officers, at a number of centres on the control of American Foul Brood by feeding sulphonamides in sucrose syrup. Promising results were obtained in most instances and of the thirty-two colonies involved in these trials all but three were reported to be free from all visible signs of disease at the end of the season.

Of the three cases in which satisfactory results were not obtained, two failed to respond to treatment and the third colony which was reported to be healthy following treatment showed a recurrence of the disease six weeks later. Further work will have to be done before a satisfactory opinion of the value of this treatment can be given.

NIXON (H. L.), RIBBANDS (C. R.). — 1952. **Food transmission in the honeybee community.** (*Proc. roy. Soc. B.*, **140**, 43-50.)

Six bees were trained to a dish, from which they collected 20 ml. of sugar syrup containing radioactive phosphorus. The distribution of radioactivity among the bees and larvae of their colony of 24,500 adults was then studied.

62 per cent of the foragers and 16-21 per cent of all the bees in the hive were radioactive within 4 hours. 76 per cent of the foragers and 43-60 per cent of all the bees were radioactive within 27 hours. The nurse bees were significantly less radioactive than the house bees and the foragers significantly more so. Within 48 hours all the large larvae in the unsealed cells were radioactive. The results are attributed to widespread food transmission.

It is suggested that food transmission is the foundation of the division of labour within the honeybee community, and of the similar odour produced by the members of each colony which serves for mutual recognition.

Food transmission would enable slow-acting insecticides contained in their food to be widely distributed among the members of a honeybee community.

O'Rourke (F. J.). — 1940. **Dates for Swarming Ants 1939.** (*Ir. Nat. Jour.*, 7 (9), 249.) — 1940. **Notes on the Ant Fauna of Howth, Co. Dublin.** (*Ir. Nat. Jour.*, 7 (10), 30.) — 1943. **Early Appearance of Bumble Bees.** (*Ir. Nat. Jour.*, 8 (4), 111.) — 1945. **Method used by Wasps of the genus *Vespa* in killing Prey.** (*Ir. Nat. Jour.*, 8, (7), 238-241.) — 1945. **A Further Extension of the Range of *Myrmica schenki*, Emery.** (*Ent. Rec.*, 57 (7/8), 85.) — 1946. **The Occurrence of Three Mermithogynes at Roundstone, Connemara, with notes on the Ants of the Area.** (*Ent. Rec.*, 58 (5), 65-70.)

This paper records the first cases of infection with the nematode parasite *Mermis* in Irish ants. One *Acanthomyops niger* female and two *L. flavus* females were found infected and are described. Information is given on the ants found in the Roundstone area with particular reference to swarming.

1946. **The Discovery of the Rare Ant *Stenamma westwoodi* West. in Co. Wicklow.** (*Ir. Nat. Jour.*, 8, 413.) — 1947. **The Rate of Progression in Ants.** (*Ent. Rec.*, 59 (1), 2-3.)

The time taken by females and workers of the species *Tetramorium caespitum* in covering 50 cms is recorded. It is noted that, while there is little variation between the speeds of the females, there is a marked difference between the speeds shown by different workers, the speed of the fastest being almost twice that of the slowest. The relationship between this finding and Chen's report on leaders and followers among ants is discussed.

1947. ***Lasius* spp. Swarming at Cambridge.** (*Ent. Mon. Mag.*, 83 (2), 41.)

On August 4th, 1946, at Parker's Piece, Cambridge, swarming began at 2.20 p.m. (G. M. T.) at 67° F. with a barometric pressure of 29.60 inches. Males constituted 90 % of the swarm at 2.20 p.m. but by 6.00 p.m. the swarm was almost entirely dealated females, at a density of 4 per sq. yard. Of the 38 females taken, 24 were *L. niger*, 14 were *L. flavus*.

1947. **The Climbing rate of the Ant *F. rufa* in Switzerland.** (*Ent. Rec.*, 59, 115-116.) —

1948. **A *Lasius mixtus* Nyl. Pterergate from Co. Wicklow.** (*Ent. Mon. Mag.*, 84, 8-9.)

The twentieth known Pterergate is described from a specimen collected at Glenmalur, Co. Wicklow, on August 11th, 1945, by Mr. D. P. Walls. A figure is given of this species and the previous literature is reviewed.

1949. **Some Ant Swarming Records from Co. Dublin.** (*Ent. Rec.*, 61, 63-65.)

Attention is drawn to how little information is available concerning the swarming habits of the ants of these islands. Information is given concerning the swarming of *Myrmica rubra*, *Lasius flavus* and *L. niger* in Co. Dublin.

1950. **The Isopod *Platyarthrus hoffmanseggi* Brandt and its relation to Ants.** (*Ent. Rec.*, 61, 63-65.)

Brook's work on the behaviour of the Isopod *Platyarthrus hoffmanseggi* in a gradient of formic acid is confirmed and illustrated by a figure. It is shown that Brook's theory, that the isopod is attracted to ants' nests by the odour of formic acid, is untenable. It is suggested that the preference shown by the isopod for the odour of formic acid is a persistence of an adaptation to the odour of *Formicine* ants to whose nests it originally came as an inquiline. At first it was limited to *Formicine* nests, but at a later stage of its evolution developed its panmyrmecophilous habits. It is, therefore, of great interest that the original adaptation should persist in specimens taken from both *Myrmicine* and *Formicine* (formic acid secreting) nests on both sides of the Atlantic.

1950. **The Distribution and General Ecology of the Irish Formicidae.** (*Proc. R. Ir. Acad. B*, **52**, 383-410.)

This paper is an attempt to give a complete account of the information available on the Irish ants to the year 1947. The species found in Ireland are listed together with information on their vice comital distribution, ecology and swarming habits. A key is given which enables the workers and queens of all native species to be identified. The paper is illustrated by a series of eight map graphs, indicating the distribution of the rarer species.

1950. **Ants as Beneficial Insects.** (*Proc. IX Inter. Cong. Ent. Stockholm*, 941-5.)

1950. **Formic Acid Production in Ants.** (*Ann. Ent. Soc. Amer.*, **43**, 437-443.)

Previous work on formic acid production in ants is reviewed. It is shown that there is little evidence that the acid is found in ants outside the sub-family Formicinae. The results of formic acid estimations on living ants are given and they are shown to be lower than those previously recorded. It is suggested that this may be because no blank estimations were made by previous workers, and also that they used dead specimens. An unsuccessful attempt to produce a reliable method of formic acid estimation on a micro-diffusion basis is described. A qualitative colormetric method is described which will detect as little as 50 γ of formic acid. It did not prove to be successful as a quantitative method. Four possible modes of formic acid synthesis in the ant are suggested and discussed.

1950. **Myrmecological Notes from Narvik, Northern Norway.** (*Tromsø, Museums Arshefter*, **8**, 47-50.)

Six species of ants were found in a few hours collecting at Narvik, Nnø division of Nordland, Norway, where hitherto only two species had been found. Those not previously recorded from Nnø are *Myrmica rubra*, *M. laevinodis*, *M. sulcinodis* and *Formica fusca*. An account is given of a swarm of *M. rubra*.

1952. **A Preliminary Ecological Classification of Ant Communities in Ireland.** (*Ent. Gaz.*, **3**, 69-72.)

Three main ecological communities may be recognized in Ireland, (a) low soil humidity fauna; (b) medium soil humidity fauna; (c) high soil humidity fauna. The species characteristic of these different ant faunas are described. The physiological basis of the distribution of the various species is discussed.

1953. **Stung by 100 Yellow Jackets.** (*J. Amer. Med. Assoc.*, **151**, 878.)

1954. **The Brown Trout (*Salmo trutta* L.) Feeding on Ants.** (*Entomol. Gazette*, **5**, 48-51.)

A collection of nearly 800 trout stomachs were examined from the river Liffey. One hundred and sixty ants were found in thirty four of these stomachs. In six of thirty four stomachs, ants formed the dominant food. The importance of examining fish stomachs from areas in which the ant fauna is unknown is indicated by the fact that of the 15 species known to occur in the counties within the Liffey River basin; no fewer than six species were found in the stomachs. Since three or four of the fifteen species are very rare, one may say that nearly half the ant species in the area occurred in a sample of about 800 trout stomachs. This shows that the examination of freshwater fish stomachs (especially if taken during the swarming season) might throw considerable light on the ant fauna of areas from which specimens might not otherwise be available.

RIBBANDS (C. R.). — 1949. **The foraging methods of individual honeybees.** (*J. Anim. Ecol.*, **18**, 47-66.)

The movements of individually marked foragers were recorded from day to day, and a few selected bees were watched continuously for periods of a day or more. The following conclusions have been drawn:

(a) The basic principle underlying the foraging behaviour pattern is the exhibition of trial and error learning of considerable complexity. The honeybee continuously chooses the best of any alternative crops with which she becomes acquainted, and compares present crops with her memory of past crops.

(b) A bee usually attaches herself to a particular area of the most profitable crop found. The size of this foraging area varies considerably.

(c) Honeybees may use choice and memory in order to select the most suitable blossoms of the crop they are working, in order gradually to change the position of the foraging area, when working two crops at once or when working one crop and inspecting another, when working two crops at different times of the day, when crops are failing, and when changing crops. Some foragers exhibit a centripetal tendency which is considered to be a consequence of the interplay between choice and memory.

(d) Attachment to a particular crop may be of any duration, from a few visits to a lifetime. The proportion of changes of attachment varies greatly with local circumstances, since behaviour is very liable and readily adaptable to changing conditions.

RIBBANDS (C. R.). — 1950. **Autumn feeding of honeybee colonies.** (*Bee World*, **31**, 74-76.)

Concentrated (66 per cent) sugar syrup, fed to colonies of honeybees in autumn, results in the production of about one-third more ripe stores than does the same weight of sugar fed as dilute (38 per cent) syrup.

The elimination by the bees of each 1 lb. of surplus water from the syrup involved the utilisation of 4.5 oz. of the syrup. This wastage of syrup was not due to brood rearing, which was less when dilute syrup was fed. About 10 per cent more ripe stores resulted from the feeding of concentrated syrup in mid-September than from the feeding of the same amount in August.

RIBBANDS (C. R.). — 1950. **Changes in the behaviour of honeybees following their recovery from anaesthesia.** (*J. Exp. Biol.*, **27**, 302-310.)

Anaesthesia with chloroform had no effect upon the memory, subsequent foraging behaviour, or longevity of worker honeybees. Anaesthesia with carbon dioxide did not impair the memory but induced a permanent change in the behaviour of worker honeybees, thus the pollen collecting tendencies of bees so treated were either eliminated or markedly reduced. The treatment of newly emerged worker bees with carbon dioxide resulted in a reduction in their brood rearing and wax secreting activities, and caused them to commence to forage at an early age. The treatment had no direct effect upon the longevity of the bees concerned.

The effects of nitrogen anaesthesia were similar to those of carbon dioxide. The factor common to both these treatments is lack of oxygen.

RIBBANDS (C. R.). — 1951. **The flight range of the honeybee.** (*J. Anim. Ecol.*, **20**, 220-226.)

The gains in weight of groups of colonies sited on the edges of crops were compared with those of groups of colonies sited $\frac{3}{8}$ and $\frac{3}{4}$ mile away from the same crops.

The chief crops chosen were apple, lime and heather; the experiments were repeated in two successive years. The effect of increased flying distance was large, and increasingly detrimental, but the magnitude of the effect varied considerably. Most of the effect was a consequence of unfavourable weather. The result illustrates a disadvantage of placing large numbers of colonies in one apiary.

RIBBANDS (C. R.). — 1952. **Division of labour in the honeybee community.** (*Proc. R. Soc. B.*, **140**, 32-43.)

Newly emerged bees in a colony were individually marked and their foraging activities were studied by subsequent observations at the hive entrance.

A few individuals gathered pollen throughout their foraging lives; many gathered none at all. Most gathered pollen at some time, but there was great diversity in the part of the foraging life at which this occurred.

There was considerable variation in the age at which different bees, emerging on the same day and living in the same colony, commenced foraging; this age ranged from 9-35 days. This variation was produced not only by alteration of the duration of the various hive duties, but also by omission of some of them. Such variation indicates that the division of labour is not determined by the age of the available workers, but is controlled by the requirements of the colony, the ages of the bees playing a subsidiary rôle.

The requirements of the colony are determined by its food supply and they are appreciated by the individual as a consequence of widespread food transmission. Food transmission is, therefore, the most primitive and important method of communication in the honeybee colony.

RIBBANDS (C. R.). — 1952. **The relation between the foraging range of honeybees and their honey production.** (*Bee World*, **33**, 2.)

The gains in weight of groups of colonies sited on the edges of crops were compared with those of groups of colonies sited $\frac{3}{8}$ and $\frac{3}{4}$ mile away from the same crops. The experiments were repeated in two successive years. The effect of increased flying distance was large and detrimental, but its magnitude varied considerably. Most of the effect was due to weather conditions.

The results emphasize the importance of foraging range, and demonstrate how slight differences in apiary position or weather may cause the complete loss of a honey crop. They illustrate the advantages of moving colonies of bees to suitable crops and of using small apiaries.

RIBBANDS (C. R.). — 1952. **The inability of honeybees to communicate colours.** (*Brit. J. anim. Behav.*, **1**, 5-6.)

Experiments determined that dancing foragers which can communicate the scent and whereabouts of a crop to other members of their colony do not convey any information concerning the colour of the flowers of the crop.

RIBBANDS (C. R.), KALMUS (H.), NIXON (H. L.). — 1952. **New evidence of communication in the honeybee colony.** (*Nature Lond.*, **170**, 438. Reprinted in *Bee World*, **33**.)

An article based upon the three papers summarized above and published in *Proc. Roy. Soc. B.*, **140**, 32.

RIBBANDS (C. R.). — 1953. **The behaviour and social life of honeybees.** (*Book-London: Bee Research Association Ltd.*)

RIBBANDS (C. R.), SPEIRS (N.). — 1953. **The adaptability of the homecoming honeybee.** (*Brit. J. anim. Behav.*, **1**, 59.)

Groups of foraging bees of known ages were marked individually and introduced to a colony of bees. One to five days later the broodchamber housing this colony was turned through 90° and changed in height. Two days later it was turned through a further 90° and its height was changed again. The marked bees reorientated quickly and completely in these experiments, and their age had no effect upon their adaptability. Colony odour facilitated reorientation.

RIBBANDS (C. R.). — 1954. **Nitrous oxide anaesthesia does not encourage reorientation of honeybees.** (*Bee World*, **35**, 91.)

Fully controlled experiments showed that anaesthesia with either "ammonium nitrate fumes" or nitrous oxide had no effect on orientation. After carbon dioxide anaesthesia *more* bees returned to their original home. All the foragers from a nucleus

which is taken from and placed near to its parent colony are likely to return to the latter, whether they have been anaesthetized or not; a variable proportion of the nucleus will consist of non-foragers, who are likely to remain in it.

RIBBANDS (C. R.). — 1954. **The defence of the honeybee community.** (*Proc. Roy. Soc. B.*, **142**, 154.)

Pairs of colonies of differently coloured bees were placed with their entrances only 2 inches apart, and many bees tried to join the wrong colony, as if it were their own. Strangers were recognised by their different scent, and their reception varied according to foraging conditions. During "nectar flows" there was no hostility, and the bees of both colonies mingled indiscriminately. In fairly good conditions there was no hostility, but partial separation was maintained through the discrimination shown by incoming foragers. In dearth conditions, when bees try to rob other colonies, all-strangers were received with hostility; most were thrown out, and many were killed. In dearth conditions marked foragers from one of the two colonies were fed with sugar syrup, but they were nevertheless repelled when they tried to enter the hive of the unfed colony; on the other hand, unfed strangers were more readily admitted into the fed colony. Thus hostility to strangers increased when forage was scarce; the condition of the community whose hive was to be entered was important, but the carriage of food by the intruder was not. These results are discussed in relation to defence of the community against both robber bees and strange queens.

RYLE (M.). — 1954. **The influence of nitrate, phosphate and potash on the secretion of nectar. Parts I and II.** (*J. agric. Sci.*, **44** (4), 400-19.)

These two papers describe the results of work on the effect of fertilizer treatment on nectar secretion in mustard, buckwheat, apple and red clover. It has been shown that in the case of apple-trees the mean quantity of sugar produced per flower can be significantly increased by extra potash. In experiments with the other plants mentioned it was found that any treatment which checked growth at flowering time, apart from a shortage of potash, increased the yield of nectar.

SIMPSON (J.). — 1948. **A Hornet's Nest.** (*Ent. Mon. Mag.*, **84**, 128-129.)

A description of the structure, and composition of the population throughout its existence, of a hornets' nest.

SIMPSON (J.). — 1949. **Humidity in the winter cluster of a colony of honeybees.** (*Bee World*, **31** (6), 41-43.)

Outside weather conditions have little effect on the humidity within a winter cluster at moderate winter temperatures. High external humidities can only affect the colony by causing water vapour discharged from the cluster to condense within the hive.

The atmosphere in a cluster containing brood has a lower saturation deficiency than that found in the same cluster without brood. The absolute humidity of the atmosphere varies from point to point in the cluster, and in general follows the temperature in such a way that throughout much of the cluster the saturation deficiency only varies within small limits.

SIMPSON (J.). — 1952. **The composition of the stores produced by bees from sugar syrup.** (*Bee World*, **33**, 112.)

The water content of stores derived from sucrose syrup was normal but the sucrose content was much higher than that of normal honey and was greater when the stores were produced from concentrated syrup than from dilute. The extent to which honey granulates is diminished by raising its sucrose content to that of stores derived from sucrose syrup. Although bees can effectively ingest *finely* granulated honey, granulation is in general undesirable, thus the presence of sucrose in syrup stores is probably beneficial.

SIMPSON (J.). — 1954. **Effects of some anaesthetics on honeybees: nitrous oxide, carbon dioxide, ammonium nitrate smoker fumes** (*Bee World*, 33, 149.)

Worker honeybees were apparently unaffected by atmospheric oxygen concentrations between 7 and 100 per cent, and only became motionless when the oxygen concentration was less than 2 per cent. The effects of nitrous oxide-oxygen mixtures differed little, if at all, from those of nitrogen-oxygen mixtures. Bees were not visibly affected by carbon dioxide concentrations up to 10-15 per cent, but became motionless if the concentration exceeded 40-45 per cent.

Fumes produced by adding ammonium nitrate to the burning fuel in a beekeeper's smoker were found to contain hydrogen cyanide or cyanogen. Their effectiveness as an anaesthetic may be due to this or to some unidentified component, but not to nitrous oxide. All these anaesthetics caused foraging bees to stop collecting pollen and accelerated the retrogression of the pharyngeal glands of young bees. The conclusion is reached that these anaesthetics do not encourage reorientation to a new hive site.

SKAIFE (S. H.). — 1953. **Sub-social Bees of the Genus *Allodape* Lep. et Serv.** (*J. Ent. Soc. S. Africa*, 16 (1).)

This deals with the life history and habits of *Allodape angulata* Brauns, *A. abdominalis* Friese and *A. halictoides* Skaife.

1954. **The Black Mound Termite of the Cape, *Amitermes atlanticus* Fuller.** (*Trans. Roy. Soc. S. Africa*, 34 (1).)

Methods of study, annual cycle and habits of *A. atlanticus*.

1954. **Caste differentiation among termites.** (*Trans. Roy. S. Africa*, 34 (2).)

Methods of study and conclusions concerning caste differentiation in *Amitermes atlanticus*.

1954. **The Food the Black Mound Termite of the Cape. *Amitermes*.** (*J. Ent. Soc. S. Africa*, 17 (1).)

Methods of study and details of feeding habits of *A. atlanticus*.

1955. **The Argentine Ant. *Iridomyrmex humilis* Mayr.** (*Presidential Address. Trans. Roy. Soc. S. Africa*, 34 (3).)

A new method of keeping these ants in the lab. is described and then the habits, life history and annual cycle under South African conditions are dealt with. Methods of control are compared.

1955. **Dwellers in Darkness. An introduction to the study of termites.** (*Longmans Green and Co. London*.)

An account in plain, everyday language of the results of twenty years' investigations of *Amitermes atlanticus*.

SYNGE (A. D.). — 1947. **Pollen collection by honeybees.** (*J. anim. Ecol.*, 16, 122-38.)

Pollen collected daily from colonies of bees by means of pollen traps was analysed. Almost 50 per cent of the pollen collected in Harpenden during the season was found to come from the clovers. A correlation between the number of loads of Red Clover pollen gathered by the bees and the daily maximum temperature was found, and this was shown to be due mainly to the increased number of red clover flowers opening at the higher temperatures. The floral mechanism making pollen available to the bee was investigated for a number of flowers including red and white clovers, *Vicia faba*, *Papaver rhoeas*, *Epilobium angustifolium* and *Brassica alba*.

Large differences in the amounts of pollen gathered from different plant species were found between two neighbouring colonies in the same apiary.

LE CONGRÈS D'ENTOMOLOGIE DE MONTRÉAL

Qu'il soit permis au Secrétaire de l'Union, avant tout compte rendu, de remercier chaleureusement les organisateurs du X^e Congrès International d'Entomologie, qui ont bien voulu réserver une vie officielle à l'U. I. E. I. S. dans le cadre du Congrès. Cette vie s'est manifestée par de nombreuses prises de contact personnelles, ainsi que par la tenue de 4 symposia et d'une assemblée générale.

L'ensemble de ces manifestations a permis de mieux mesurer le chemin parcouru depuis le IV^e Congrès d'Entomologie d'Amsterdam, où l'idée de l'Union a pris corps.

Vie des Sections.

— Beaucoup de membres nord-américains de l'Union étaient présents et les 3 symposia organisés par leur section connurent un grand succès. Seule l'absence du Professeur SCHNEIRLA, retenu par son travail sur le terrain, fut regrettée de tous.

— Les sections sud-américaines, représentées par le Père J. S. MOURE, ont fait part des difficultés qu'elles rencontrent pour acquitter légalement leurs cotisations.

— Les sections européennes étaient moins bien représentées que les sections américaines ; l'absence de membres allemands et italiens de l'Union a été vivement regrettée.

— Une section nouvelle est née au cours du Congrès, et tous les membres de l'Union s'en féliciteront : c'est la section soviétique. Trois membres ont été inscrits officiellement : MM. STEINBERG, MONTCHADSKY, POPOV (Zoological Institute, Academy of Sciences of the U. S. S. R., Leningrad 164, U. S. S. R.). M. STEINBERG s'occupe de l'organisation de la nouvelle section ; il espère que plusieurs collègues soviétiques participeront à notre prochain Congrès.

— M. BAETA NEVES (Institut Supérieur d'Agronomie Tapeda de Ajuda, Lisbonne, Portugal) a accepté de centraliser, pour le Portugal, toutes les informations concernant l'Union, mais peu de Portugais s'intéressent aux Insectes Sociaux.

— M. A. P. KAPUR [Entomology section Zoological Survey of India (Indian Museum), Calcutt 12, India] a promis de proposer à ses collègues la création d'une section pour l'Inde.

SYMPOSIA.

I. — Symposia organisés par le Congrès et la Section nord-américaine de l'U. I. E. I. S. (Evolution of social life in Insects).

Trois demi-journées ont été consacrées à ces symposia ; les communications suivantes ont été lues :

HARRIS (W. V.). — *Colony formation in the Isoptera.*

MICHENER (C. D.). — *Evolution of social behavior in bees.*

EVANS (H. E.). — *Evolution of social life in wasps.*

WEBER (N. E.). — *Social evolution in ants with particular reference to fungus growing patterns.*

TREAT (A. E.). — *Social organisation in the moth ear mite Myrmonyssus phalaenodectes.*

MOURE (J. S.), PAULO NOGUEIRA-NETO, KERR (W. E.). — *Behaviour of social bees, principally Meliponinae.*

FLANDERS (S. E.). — *The regulation of caste ratios in the social hymenoptera.*

BRIAN (M. V.). — *The evolution of queen control.*

LE MASNE (G.). — *Recherches sur les Fourmis parasites : un cas de parasitisme social double.*

EISNER (T.), BROWN (W. L., Jr.). — *Food transmission and the evolution of ants. I. The proventriculus.*

WILSON (E. O.), EISNER (T.). — *Food transmission and the evolution of ants. II. Radioactive tracer studies.*

II. — Symposium organisé par le Congrès et les sections européennes de l'U. I. E. I. S. (Les constructions sociales chez les Insectes).

Ce symposium a duré une demi-journée ; les communications suivantes ont été lues :

GRASSÉ (P. P.), NOIROT (Ch.). — *La construction chez les Macrotermittinæ (Termites champignonnistes).*

LEDoux (A.). — *La construction du nid chez quelques Fourmis arboricoles de France et d'Afrique tropicale.*

DARCHEN (R.). — *La régulation des constructions chez l'Abeille Apis mellifica.*

BRIAN (M. V.). — *The nests of some British ants.*

RICHARDS (O. W.). — *The nests of South american wasps.*

ASSEMBLÉE GÉNÉRALE.

Une assemblée générale des membres de l'U. I. E. I. S. présents au Congrès de Montréal s'est tenue le jeudi 23 août, à 9 heures, sous la présidence de M. Pierre P. GRASSÉ.

Ordre du jour : Fixation de la date du Congrès de 1957.

M. GRASSÉ expose les raisons qui ont amené la Commission française d'Organisation à choisir les dates du 9 au 13 juillet 1957 pour la tenue du Congrès :

— Facilités de séjour tant à Paris qu'en province (excursion après le Congrès) plus grandes à cette époque de l'année.

— La faune entomologique rencontrée au cours des excursions est plus abondante et variée qu'au mois d'août.

— Cette période est plus favorable à la participation d'un grand nombre de collègues américains, britanniques et français.

Cependant, M. le Professeur GÖSSWALD avait demandé par lettre à M. GRASSÉ de retarder le Congrès d'une quinzaine de jours, ce qui faciliterait les déplacements des collègues allemands.

Une discussion s'ouvre après cet exposé de faits :

M. MICHENER pense que les Américains seront relativement peu nombreux au Congrès ; le problème des dates concerne donc surtout les Européens. Toutefois, les mois de juin, juillet, août et septembre sont favorables aux déplacements des collègues nord-américains.

Le Père MOURE pense que le mois de juillet est le meilleur moment pour les collègues sud-américains.

M. STEINBERG, représentant la nouvelle section soviétique de l'Union, pense que les mois de juillet et d'août conviennent à tous ses collègues.

M. HERRING, appelé avec voix consultative pour représenter les entomologistes allemands en l'absence de membres de la section allemande de l'Union, pense que les difficultés de ses collègues ne sont pas insurmontables et que les raisons exposées par M. GRASSÉ sont déterminantes.

M. HARRIS donne l'accord des collègues britanniques pour les dates proposées et suggère que l'assemblée les accepte sans discuter plus longuement, car les dates d'un Congrès International ne peuvent jamais satisfaire tout le monde.

L'assemblée adopte alors à l'unanimité les dates proposées par le Comité d'Organisation français : le Congrès se tiendra à Paris du 9 au 13 juillet 1957 et sera suivi d'une excursion dans le Sud-Ouest de la France, qui durera environ six jours.

INTERNATIONAL UNION FOR THE STUDY
OF SOCIAL INSECTS NORTH AMERICAN SECTION

Two symposia on the social insects to be sponsored at the 1956 annual meeting of the American Assoc. for the Advancement of Science, to be held in New York City, Dec. 26-30, 1956.

Wed., Dec. 26, 2:00 p.m. ; Penn Top, Hotel Statler.

Symposium I. — Communication in Insects : Perspective on Fact and Theory (arr. by T. C. Schneirla).

WILLIAM S. CREIGHTON, *City College of New York, Presiding.*

1. Communicative Dancing by Insects. Vincent G. DETHIER, Johns Hopkins University. (Lantern, 30 min.)
2. Insect Communication by the Medium of Food Distribution. Edward O. WILSON, Harvard University. (Lantern, 20 min.)
3. Mechanisms of Communication in Ants. Arthur C. COLE, University of Tennessee. (Lantern, 30 min.)
4. Contrasting Patterns in Ants, and Theoretical Remarks. T. C. SCHNEIRLA, American Museum of Natural History. (Lantern, 30 min.)

Discussants : J. A. DOWNES, Science Service, Division of Entomology, Ottawa, Canada ;

Neal A. WEBER, Swarthmore College ;

John B. CALHOUN, National Institute of Mental Health.

Thursday., Dec. 27, 9:00 a.m. ; West Room, Hotel Statler.

Symposium II. — Communication in Insects : Problems and Methods (arr. by T. C. Schneirla).

KENNETH D. ROEDER, *Tufts University, Presiding.*

1. Chemoreceptive Mechanisms. Edward S. HODGSON, Columbia University. (Lantern, 30 min.)
2. Sensory Factors in the Orientation of Moths. Ilse SCHWINCK, New York University, College of Medicine. (Lantern, 30 min.)

3. Phonoreception. Asher E. TREAT, City College of New York. (Lantern, 30 min.)
4. Steering Mechanisms. Horst MITTELSTAEDT, Max-Planck Institut, Wilhelmshaven. (Lantern, 30 min.)

Discussant : William Van der Kloot, Harvard University ;
Talbot WATERMAN, Yale University.

TABLE ALPHABÉTIQUE DES AUTEURS

ALTMANN (G.). — Die Regulation des Wasserhaushaltes der Honigbiene.....	33
BACK (Erika). — Einfluß der im Pollen enthaltenen Vitamine auf Lebensdauer, Ausbildung der Pharynxdrüsen und Brutfähigkeit der Honigbiene.....	285
BIER (Karlheinz). — Arbeiterinnenfertilität und Aufzucht von Geschlechtstieren als Regulationsleistung des Ameisenstaates	177
BOISTEL (J.), LECOMTE (J.) et CORABŒUF (E.). — Quelques aspects de l'étude électrophysiologique des récepteurs sensoriels des antennes d'hyménoptères.	25
BRIAN (M. V.). — Inefficiency in brood-rearing in the ant <i>Myrmica Rubra</i> L..	71
BRIAN (M. V.). — The natural density of <i>Myrmica Rubra</i> and associated ants in West Scotland	473
BRIAN (M. V.). — Studies of Caste differentiation in <i>Myrmica Rubra</i> L. — 4. Controlled larval nutrition	369
BROWN (William L.). — Notes on the ant genus <i>holcoponera mayr</i> , with descriptions of two new species	489
BROWN (W. L.) v. <i>Wilson</i> .	
BUCHLI (Harro). — Le cycle de développement des castes chez <i>Reticulitermes</i> .	395
BUCHLI (Harro). — Die Neotenie bei <i>Reticulitermes</i>	131
BUSNEL (René-Guy). — Étude de l'un des caractères physiques essentiels des signaux acoustiques réactogènes artificiels sur les orthoptères et d'autres groupes d'insectes	11
CHAUVIN (Rémy). — Les facteurs qui gouvernent la ponte chez la reine des abeilles.....	499
CORABŒUF (E.), v. <i>J. Boistel</i> .	
DARCHEN (Roger). — La construction sociale chez <i>Apis mellifica</i>	293
DESNEUX (Jules). — Structures « atypiques » dans les nidifications souterraines d' <i>Apicotermes Lamani</i> Sj. (<i>Isoptera</i> , <i>Termitidæ</i>) mises en évidence par la radiographie	277
ERNST (E.). — Die Reaktionen von vier Termitenarten in der Feuchtigkeitsorgel.	229
FLANDERS (S. E.). — The mechanisms of sex-ratio regulation in the (parasitic) hymenoptera	325
FORBES (James). — Observations on the gastral digestive tract in the male Carpenter ant, <i>Camponotus Pennsylvanicus</i> degeer (<i>Formicidæ</i> , <i>Hymenoptera</i>).	505
GERVET (M. Jacques). — L'action des températures différentes sur la monogynie fonctionnelle chez les polistes (<i>Hyménoptères Vespides</i>).....	159
GLÖCKNER (Wolfgang E.). — Ueber Zentrifugerversuche an Formiciden....	403
GÖTZE (G.). — Methodik der Selektion der Honigbiene auf Langrüsseligkeit.	335
GONTARSKI (H.). — Der Nachschaffungsinstitut beim Bienenvolk	347
GÖSSWALD (Karl). — Begrüßungsansprache anlaßlich der Eröffnung des II. Internationalen Kongresses (3-6 April 1955) in Würzburg.....	7

GRASSÉ (P.). — Discours d'ouverture du II ^e Congrès de l'Union internationale pour l'Étude des Insectes sociaux.....	3
HARRIS (W. V.). — Termite mound building.....	261
HÜSING (J. O.). — Weitere Beobachtungen über die Nahrung von Vespiden-Larven.....	41
JEFFREE (Edward P.). — Winter brood and pollen in honeybee colonies.....	417
JOLY (P.). — Croissance et indices de grégariation chez <i>Locusta migratoria</i> L.....	16
JUCCI (Carlo). — Ricerche Sulle ghiandole endocrine nelle termiti un nuovo Campo di Studio : La endocrinologia Comparata degli isotteri.....	283
KALSHOVEN (L. G. E.). — Observations on the inner Structure of <i>Macrotermes Gilvus</i> mounds in Java.....	269
KALSHOVEN (L. G. E.). — Observations on <i>Macrotermes Gilvus</i> Holmgr. in Java. 3. Accumulations of finely cut vegetable matter in the nests.....	455
KERR (W. E.), SANTOS NETO (G. R. Dos). — Contribuição para o Conhecimento da bionomia dos meliponini. — 5. Divisão de trabalho entre as operarias de <i>Melipona Quadrifasciata Quadrifasciata</i> Lep.	423
KOCH (Anton) und ILSE SCHWARZ. — Wirkstoffe der B-Gruppe in der Bienen-nahrung.....	213
LECOMTE (Jacques). — Nouvelles recherches sur l'interattraction chez <i>Apis mellifica</i> L.	195
LECOMTE (J.), v. J. Boistel.	
LE MASNE (G.). — La signification des reproducteurs aptères chez la Fourmi <i>Ponera Eduardi</i> Forel. I. Le Polymorphisme des mâles chez les Fourmis..	239
LUKOSCHUS (Fritz). — Stoffwechselstimulierende Hormone als Ursache des Verhaltens der Honigbiene bei der Aufzucht von Geschlechtstieren.....	185
LÜSCHER (Martin). — Die Entstehung von Ersatzgeschlechtstieren bei der Termite <i>Kaloterme flavicollis</i> Fabr.	119
LÜSCHER (Martin). — Die Lüfterneuerung im Nest der Termite <i>Macrotermes natalensis</i> (Haviland).....	273
MEYER (Waltraud). — Arbeitsteilung im Bienenschwarm.....	303
MÜLLER (Hans). — Der Massen-Wechsel einiger Honigtau liefernden Baum-lause im Jahre 1954.....	75
NOIROT (Ch.). — Les sexués de remplacement chez les Termites supérieurs (<i>Termitidae</i>).....	145
O'ROURKE (Fergus J.). — The medical and veterinary importance of the formi-cidae.....	107
PAIN (Janine). — Sur l'ectohormone des reines d'abeilles.....	199
PICKENS (A. L.). — Links and gaps in the common castes of termites.....	233
RHEIN (Werner V.). — Ueber die Ernährung der Arbeitermade von <i>Apis melli-fica</i> L., insbesondere in der Atersperiode.....	203
RUTTNER (Friedrich). — Zur Frage der Spermaübertragung bei der Bienenkönigin.	351
SAKAGAMI (Shoichi F.) und TAKAHASHI (Hiroya). — Beobachtungen neber die Gynandromorphen Honigbienen, mit besonderer Berücksichtigung ihrer Handlungen innerhalb des Volkes.....	513
SANDS (W. A.). — Some factors affecting the survival of odontotermes Badius.	531
SANTOS NETO (G. R. Dos), v. Kerr (W. E.).	
SCHMIDT (H.). — Einige Bemerkungen über die Ersatzgeschlechtstiere von <i>Reticulitermes</i>	129
SCHNEIRLA (T. C.). — A preliminary survey of colony division and related processes in two species of terrestrial army ants.....	49

SCHWARZ (Ilse), v. <i>Anton Koch</i> .	
SOULIÉ (J.). — Le déclenchement et la rupture de l'état d'hibernation chez <i>Cremastogaster scutellaris</i> Ol. (<i>Hymenoptera</i> , <i>Formicoidea</i>)	431
SOULIÉ (J.). — La nidification chez les espèces françaises du genre <i>Cremastogaster</i> Lund (<i>Hymenoptera</i> , <i>Formicoidea</i>)	93
TAKAHASHI (Hiroya), v. <i>Sakagami (Shoichi F.)</i> .	
WEAVER (Nevin). — The foraging behavior of honeybees on hairy vetch, foraging methods and learning to forage.....	537
WILSON (E. O.) and BROWN (W. L., Jr.). — New parasitic ants of the genus <i>Kyidris</i> , with notes on ecology and behavior.....	439

TABLE DES MATIÈRES

CONTENUES DANS LE TOME III 1956

Numéro I.

II^e CONGRÈS DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX.

Discours d'ouverture du Congrès, par P. GRASSÉ	3
Discours d'ouverture du Congrès, par Karl GOSSWALD	8
Étude de l'un des caractères physiques essentiels des signaux acoustiques réactogènes artificiels sur les orthoptères et d'autres groupes d'insectes, par René-Guy BUSNEL	11
Croissance et indices de grégarisation chez <i>Locusta migratoria</i> L., par P. JOLY	17
Quelques aspects de l'étude électrophysiologique des récepteurs sensoriels des antennes d'Hyménoptères, par J. BOISTEL, J. LECOMTE, E. CORABŒUF ...	25
Die Regulation des Wasserhaushaltes der Honigbiene, von Dr O. ALTMANN ..	33
Weitere Beobachtungen über die Nahrung von Vespiden-Larven, von J. O. HUSING	41
A preliminary survey of colony division and related processes in two species of terrestrial army ants, by T. C. SCHNEIRLA.....	49
Inefficiency in brood-rearing in the ant <i>Myrmica Rubra</i> L., by M. V. BRIAN ..	71
Der Massenwechsel einiger Honigtau liefernden Baumläuse im Jahre 1954, von Hans MÜLLER	75
La nidification chez les espèces françaises du genre <i>Cremastogaster</i> Lund (<i>Hymenoptera</i> — <i>Formicoidea</i>), par J. SOULIÉ	93
The medical and veterinary importance of the formicidae, by Fergus J. O'Rourke ..	107
Die Entstehung von Ersatzgeschlechtstieren bei der Termiten <i>Kaloterme flavicollis</i> Fabr., von Martin LÜSCHER	119
Einige Bemerkungen über die Ersatzgeschlechtstiere von <i>Reticulitermes</i> , H. SCHMIDT.....	129
Die Neotenie bei <i>Reticulitermes</i> , von Harro BUCHLI.....	131
Les sexués de remplacement chez les Termites supérieurs (<i>Termitidae</i>), par Ch. NOIROT	145
L'action des températures différentielles sur la monogynie fonctionnelle chez les polistes (Hyménoptères vespides), par M. Jacques GERVET	159
Arbeiterinnenfertilität und Aufzucht von Geschlechtstieren als Regulationsleistung des Ameisenstaates, von Karlheinz BIER	177
Stoffwechselstimulierende Hormone als Ursache des Verhaltens der Honigbiene bei der Aufzucht von Geschlechtstieren, von Fritz LUKOSCHUS	185
Nouvelles recherches sur l'interattraction chez <i>Apis mellifica</i> L., par Jacques LECOMTE	195

Sur l'ectohormone des reines d'Abeilles, par Janine PAIN	199
Ueber die Ernährung der Arbeitermade von <i>Apis mellifica</i> L., insbesondere in der Altersperiode, von Werner v. RHEIN	203

Numéro II.

Wirfstoffe der B-Gruppe in der Bienennahrung, von Anton KOCH und Ilse SCHWARZ	213
Die Reaktionen von vier Termitenarten in der Feuchtigkeitssorgel, von E. ERNST	229
Links and Gaps in the common castes of Termites, by A. L. PICKENS	233
La signification des reproducteurs aptères chez la Fourmi <i>Ponera Eduardi</i> Forel, I. Le polymorphisme des mâles chez les Fourmis, par G. LE MASNE	239
Termite mound building, by W. V. HARRIS	261
Observations on the inner structure of <i>Macrotermes gilvus</i> mounds in Java, by L. G. E. KALSHOVEN	269
Die Lüfterneuerung im Nest der Termite <i>Macrotermes natalensis</i> (Haviland), von Martin LÜSCHER	273
Structures « atypiques » dans les nidifications souterraines d' <i>Apicotermes Lamani</i> Sj. (<i>Isoptera</i> , <i>Termitidæ</i>) mises en évidence par la radiographie, par Jules DESNEUX	277
Ricerche sulle chiandole endocrine nelle Termiti un nuovo campo di studio : La Endocrinologia comparata degli isoteri, par Carlo JUCCI	283
Einfluß der im Pollen enthaltenen Vitamine auf Lebensdauer, Ausbildung der Pharynxdrüsen und Brutfähigkeit der Honigbiene, von Erika BACK	285
La construction sociale chez <i>Apis mellifica</i> , par Roger DARCHEN	293
Arbeitsteilung im Bienenschwarm, von Waltraud MEYER	303
The mechanisms of sex-ratio regulation in the (parastici) Hymenoptera, by J. E. FLANDERS	325
Methodik der Selektion der Honigbiene auf Langrüsseligkeit, von G. GETZE	335
Der Nachschaffungsinstitut beim Bienenvolk, von H. GONTARSKI	347
Zur Frage der Spermaübertragung bei der Bienenkönigin, von Friedrich RUTTNER	351
Compte rendu de l'Assemblée générale de la Section française de l'U. I. E. I. S., Paris, 11 février 1956	361
Travaux des membres de l'Union	365

Numéro III.

Studies of Caste differentiation in <i>Myrmica rubra</i> L. 4. Controlled Larval nutrition, by M. V. BRIAN	369
Le Cycle de développement des Castes chez <i>Reticulitermes</i> , par Harro BUCHLI	395
Ueber Zentrifugerversuche an Formiciden, von Wolfgang E. GLÖCKNER	404
Winter Brood and pollen in honeybee colonies, by Edward P. JEFFREE, B. Sc.	417
Contribuição para o Conhecimento da Bionomia dos Meliponini. 5. Divisão de Trabalho entre as operarias de <i>Melipona quadrifasciata quadrifasciata</i> Lep, by W. E. KERR, G. R. dos SANTOS NETO	423
Le déclenchement et la rupture de l'État d'Hibernation, chez <i>Crématogaster scutellaris</i> Ol. (<i>Hymenoptera-Formicoidea</i>), par J. SOULIÉ	431

New Parasitic ants of the genus <i>Kyidris</i> , with notes on ecology and behavior, by E. O. WILSON and W. L. BROWN, Jr.	439
Observations on <i>Macrotermes Gilvus</i> Holmgr. In Java. Accumulations of finely cut vegetable matter in the nests (1), by L. G. E. KALSHOVEN	455
Travaux des membres de l'Union	463

Numéro IV.

The natural density of <i>Myrmica Rubra</i> and associated ants in West Scotland, by M. V. BRIAN	473
Notes on the ant genus <i>Holcaponera</i> Mayr, with descriptions of two new species, by William L. BROWN, Jr.	489
Les facteurs qui gouvernent la ponte chez la reine des Abeilles, par Rémy CHAU- VIN	499
Observations on the gastral digestive tract in the male Carpenter ant, <i>Campo- notus Pennsylvanicus</i> degeer (Formicidæ, Hymenoptera), by James FORBES.	505
Beobachtungen über die Gynandromorphen Honigbienen, mit besonderer Berücksichtigung ihrer Handlungen innerhalb des Volkes, von Shoichi F. SAKAGAMI und Hiroya TAKAHASHI	513
Some factors affecting the survival of <i>odontotermes</i> Badius, by W. A. SANDS, M.Sc.	531
The foraging behavior of honeybees on hairy vetch, foraging methods and learning to forage, by Nevin WEAVER	537

NOTE POUR LES AUTEURS

- 1° *Insectes sociaux* publie des mémoires originaux, des notes ou des revues concernant les problèmes relatifs aux insectes sociaux.
- 2° Les auteurs reçoivent gratuitement 50 tirés à part.
- 3° Les manuscrits doivent être adressés à l'un des membres du Comité de rédaction, qui les transmettra au secrétaire.
- 4° Les textes remis pour l'impression doivent être dactylographiés. Leur forme sera considérée comme définitive, et leur étendue ne pourra pas dépasser 20 pages dactylographiées (*), illustration comprise.
- 5° L'illustration des articles est libre. Toutefois le secrétaire se réserve le droit de demander la suppression des figures dont le nombre serait jugé excessif. Les figures au trait sont à la charge de la revue. Les planches, les photographies sont à la charge des auteurs, à l'exception de celles que le secrétaire jugerait pouvoir prendre au compte de la revue. Les documents doivent être fournis prêts à cliquer.
- 6° Les légendes des figures doivent être indépendantes des documents d'illustration.
- 7° Chaque article doit être accompagné d'un sommaire qui en résume les points essentiels. Il sera joint une traduction de ce sommaire en deux autres langues.
- 8° La disposition de la bibliographie doit être conforme aux règles suivantes de présentation :

Date. Nom (prénom). — Titre de l'article (titre du périodique. Année. Numéro du tome, pages de début et de fin de l'article).

- 9° Les épreuves sont adressées aux auteurs pour correction. Elles doivent être retournées SANS DÉLAI au secrétaire : G. Richard, 105, boulevard Raspail, Paris-VI^e (France).

(*) 28 lignes de 67 caractères par page.

MAR 22 1957

D IN STACKS

M
C & **ie**